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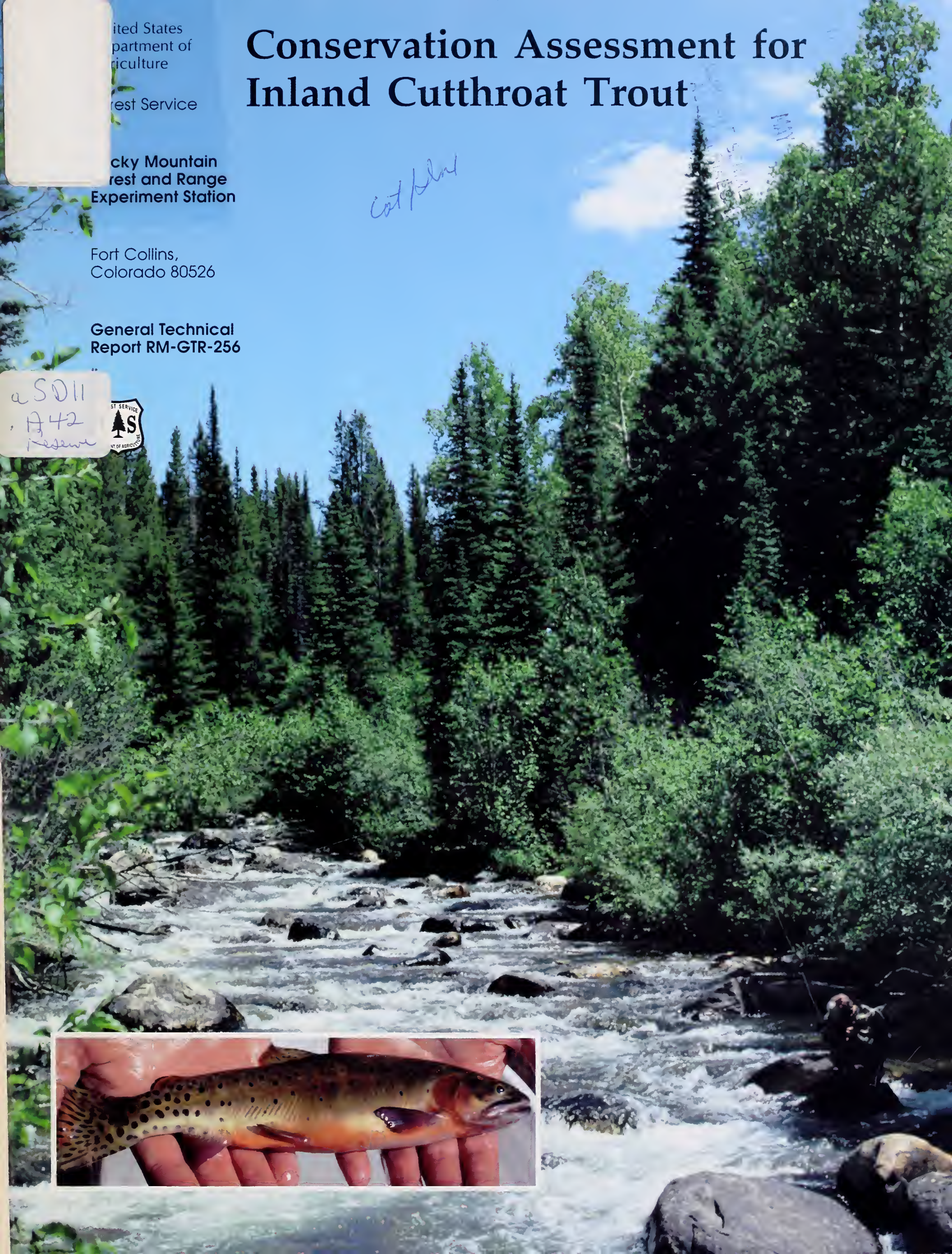
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Conservation Assessment for Inland Cutthroat Trout

Cutthroat

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Abstract

This document focuses on the state of the science for five subspecies of cutthroat trout found largely on public lands in the Rocky Mountain and Intermountain West. These subspecies are restricted to a fragment of their former range, and primarily occupy small, high-elevation streams. Little is known about the three rarest subspecies (Bonneville, Colorado River, and Rio Grande cutthroat trout), and the data on the more abundant subspecies (westslope and Yellowstone cutthroat trout) were obtained from relatively few areas. The historic diversity of life history strategies has been reduced. All subspecies have suffered from introductions of nonnative fishes, habitat degradation and fragmentation, and overfishing. Current management often centers on restrictive angling regulations, barricading streams to prevent invasion by nonnative fishes, and reintroductions into streams with existing barriers.

Keywords: cutthroat trout, *Oncorhynchus clarki*, fishing, nonnative species, mountain streams

Conservation Assessment for Inland Cutthroat Trout

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Preface

This conservation assessment for inland cutthroat trout focuses on five subspecies found largely on public lands in the Rocky Mountain and Intermountain West. Though derived from a common ancestor, these subspecies have diverged at different rates to the extent that one was proposed for elevation to full species status (Allendorf and Leary 1988) and another may be composed of up to three genetically distinguishable groups (Shiozawa and Evans 1994). The five subspecies herein were selected because they have become rare, they occupy lands under a variety of jurisdictions, and coordinated, progressive management could halt a further decline to extinction. Secure subspecies, those already listed under the Endangered Species Act, and those of uncertain taxonomic status were not considered. As the ability to recognize taxonomic differences between subspecies improves, consideration of new or existing subspecies is merited.

The primary goal of the assessment is to identify the state of the science for each subspecies. Recent treatises (Gresswell 1988; Behnke 1992) summarized portions of this knowledge, but this assessment attempts to be more comprehensive. Throughout this document, the authors sought to refrain from using information from one subspecies to interpret the biology of another. In some instances this has been unavoidable, because we are completely ignorant about certain life history characteristics (or entire life histories) of subspecies. Also, the variability in length among these chapters reflects the variability in our knowledge; not surprisingly, the most abundant subspecies are also the best studied. A companion docu-

ment that identifies the current distribution and characteristics of all known populations of each subspecies is in preparation.

A second goal of the assessment is to help managers to make informed choices about the consequences of land management for these subspecies. For some populations of certain subspecies, some of the data are available, but the habitats and life history strategies of most populations are unstudied. Inventories of fish behaviors, life histories, and distribution, coupled with genetic analyses, are necessary to identify the total phenotypic and genotypic variability of each subspecies, to recognize evolutionarily unique stocks, and to predict their response to management. Future research must center on these information gaps.

An implicit assumption in each chapter is that these native fishes are worth saving, and that we have an ethical and legal obligation to prevent them from going extinct. Though many readers may share that vision, the choice of tactics to achieve it will not be unanimous. Individuals, interest groups, states, and federal agencies will differ in their desire to see federal listing of these subspecies under the Endangered Species Act or in their willingness to forfeit some opportunities (to harvest fish, to angle for non-native fish, or to manage public lands for conflicting purposes). Because these fish are vulnerable to extinction, we encourage the open, honest involvement of everyone interested. A shared vision is the only insurance for a future for these subspecies.

Michael K. Young

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Names of Fishes

Catostomidae

<i>Catostomus ardens</i>	Utah sucker
<i>Catostomus catostomus</i>	longnose sucker
<i>Catostomus commersoni</i>	white sucker
<i>Catostomus discobolus</i>	bluehead sucker
<i>Catostomus latipinnis</i>	flannelmouth sucker
<i>Catostomus platyrhynchus</i>	mountain sucker
<i>Catostomus plebeius</i>	Rio Grande sucker
<i>Catostomus tahoensis</i>	Tahoe sucker
<i>Chasmistes liorus</i>	June sucker

Centrarchidae

<i>Micropterus</i> spp.	bass
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Cottidae

<i>Cottus bairdi</i>	mottled sculpin
<i>Cottus bairdi semiscaber</i>	Bonneville mottled sculpin
<i>Cottus extensus</i>	Bear Lake sculpin

Cyprinidae

<i>Couesius plumbeus</i>	lake chub
<i>Gila atraria</i>	Utah chub
<i>Gila bicolor</i>	tui chub
<i>Gila copei</i>	leatherside chub
<i>Gila pandora</i>	Rio Grande chub
<i>Gila robusta</i>	roundtail chub
<i>Iotichthys phlegethontis</i>	least chub
<i>Phoxinus erythrogaster</i>	southern redbelly dace
<i>Ptychocheilus lucius</i>	Colorado squawfish
<i>Ptychocheilus oregonensis</i>	northern squawfish
<i>Rhinichthys cataractae</i>	longnose dace
<i>Rhinichthys osculus</i>	speckled dace
<i>Richardsonius balteatus</i>	redside shiner
<i>Semotilus atromaculatus</i>	creek chub

Esocidae

<i>Esox lucius</i>	northern pike
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Percidae

<i>Perca flavescens</i>	yellow perch
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Salmonidae

<i>Coregonus clupeaformis</i>	lake whitefish
<i>Oncorhynchus aguabonita</i>	golden trout
<i>Oncorhynchus clarki</i> <i>bouvieri</i>	Yellowstone cutthroat trout
<i>Oncorhynchus clarki clarki</i>	coastal cutthroat trout
<i>Oncorhynchus clarki</i> <i>henshawi</i>	Lahontan cutthroat trout
<i>Oncorhynchus clarki</i> <i>lewisi</i>	westslope cutthroat trout
<i>Oncorhynchus clarki</i> <i>pleuriticus</i>	Colorado River cutthroat trout
<i>Oncorhynchus clarki</i> subsp.	fine-spotted cutthroat trout
<i>Oncorhynchus clarki utah</i>	Bonneville cutthroat trout
<i>Oncorhynchus clarki</i> <i>virginalis</i>	Rio Grande cutthroat trout
<i>Oncorhynchus gilae</i>	Gila trout
<i>Oncorhynchus gorboscha</i>	pink salmon
<i>Oncorhynchus kisutch</i>	coho salmon
<i>Oncorhynchus mykiss</i>	rainbow trout, steelhead
<i>Oncorhynchus nerka</i>	kokanee
<i>Oncorhynchus tshawytscha</i>	chinook salmon
<i>Prosopium abyssicola</i>	Bear Lake whitefish
<i>Prosopium coulteri</i>	pygmy whitefish
<i>Prosopium gemmiferum</i>	Bear Lake cisco
<i>Prosopium spilonotus</i>	Bonneville whitefish
<i>Prosopium williamsoni</i>	mountain whitefish
<i>Salmo trutta</i>	brown trout
<i>Salvelinus confluentus</i>	bull trout
<i>Salvelinus fontinalis</i>	brook trout
<i>Salvelinus namaycush</i>	lake trout
<i>Thymallus arcticus</i>	Arctic grayling

Chapter 1

Westslope Cutthroat Trout

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Introduction

The westslope cutthroat trout inhabits streams on both sides of the Continental Divide. On the east side of the divide, they are distributed mostly in Montana but also occur in some headwaters in Wyoming and southern Alberta (Behnke 1992). They are in the Missouri Basin downstream to about 60 km below Great Falls and in the headwaters of the Judith, Milk, and Marias rivers. On the west side of the Continental Divide the subspecies occurs in the upper Kootenai River; the Clark Fork drainage in Montana and Idaho downstream to the falls on the Pend Oreille River; the Spokane River above Spokane Falls; the Coeur d'Alene and St. Joe drainages; and the Clearwater and the Salmon river basins. Several disjunct populations of westslope cutthroat trout persist in the mid-Columbia River basin (Behnke 1992) in the Methow, Entiat, and Wenatchee river basins in Washington and in the John Day River in Oregon. Behnke (1992) considered all cutthroat trout native to the upper and middle Columbia, South Saskatchewan, and upper Missouri basins to be this subspecies.

Life History Characteristics

Westslope cutthroat trout are adfluvial, fluvial, or resident (with the exception of a single lake-spawning population; Carl and Stelfox 1989) (table 1). Adfluvial fish live in the large lakes in the upper Columbia drainage and spawn in lake tributaries. Fluvial fish live and grow in rivers instead of lakes, but they too immigrate to tributaries for spawning. Most adults return to the river or lake after spawning (Rieman and Apperson 1989; Behnke 1992). Resident fish complete their entire life in tributaries and seldom exceed 300 mm in length (Miller 1957; Averett 1962; Bjornn 1975; Thurow and Bjornn 1978). All three life-history forms may occur in a single basin (Averett and MacPhee 1971; Rieman and Apperson 1989).

Westslope cutthroat trout begin to mature at age 3 but usually spawn first at age 4 or 5 (table 2). Sexually maturing adfluvial fish move into the vicinity of tributaries in fall and winter where they remain until they begin to migrate upstream in the spring (Liknes 1984). They spawn from March to July at water temperatures near 10°C (Roscoe 1974; Liknes 1984; Shepard et al. 1984). A population of adult fish in the St. Joe River, Idaho, included 1.6 females for each male (Thurow and Bjornn 1978). Average length was 334 mm for females and 366 mm for males. A similar population in Big Creek, Montana, included 4.1 females for each male (Huston et al. 1984), and the average length was 381 mm for females and 386 mm for males. Ratios of females to males in other locations in Montana ranged from 1:1 to 6.2:1 (Huston et al. 1984).

Alternate-year spawning has been reported in the Flathead River basin in Montana (Shepard et al. 1984) and other populations. Repeat spawners composed from 0.7 to 24% of the adult populations (Shepard et al. 1984), although Block (1955) concluded that few fish spawn more than twice. Mortality of fish in the spawning run from Lake Koocanusa to Young Creek ranged from 27 to 60%, the rates being somewhat higher for males than for females (Huston et al. 1984).

Westslope cutthroat trout are thought to spawn predominantly in small tributaries. Migratory forms may spawn in the lower reaches of the same streams used by resident fish (Johnson 1963). Body size (migrants are larger) might influence the suitability or selection of sites related to stream size. Not all of the same tributaries used for spawning in one year may be used in the following year (Block 1955). Headwaters and upper reaches of large river basins like the Coeur d'Alene and St. Joe are typically dominated by resident and fluvial forms, but tributaries to lakes primarily support adfluvial fish (Averett and MacPhee 1971; Thurow and Bjornn 1978; Rieman and Apperson 1989).

Table 1.—Summary of life history, habitat use, population, and community information for westslope cutthroat trout. Data were summarized from Bjornn (1957), Averett (1962), Averett and MacPhee (1971), Rankel (1971), Mauser (1972), Athearn (1973), Pratt (1984b), Shepard et al. (1984), Lewynsky (1986), Hoelscher and Bjornn (1989), and Rieman and Apperson (1989).

Life history	Stream order				Habitat type
	Winter (D-J-F)	Spring (M-A-M)	Summer (J-J-A)	Fall (S-O-N)	
Total	Highest densities in 2nd and 3rd order streams				pools
Fluvial					
spawners	>3	1-4	1-4	>3	pools with overhead cover
fry	1-4	1-4	1-4	1-4	stream margins, low velocity areas, backwaters, side channels
juvenile	2-4	2-4	2-4	2-4	main channel pools
subadult	>3	>3	>3	>3	pools with overhead cover
Adfluvial					
spawners	lake	1-4	1-4	lake	same as fluvial
fry	1-4	1-4	1-4	1-4	same as fluvial
juvenile	2-4	2-4	2-4	2-4	same as fluvial
subadult	lake	lake	lake	lake	top of thermocline
Resident					
spawners	1-3	1-3	1-3	1-3	same as fluvial
fry	1-3	1-3	1-3	1-3	same as fluvial
juvenile	1-3	1-3	1-3	1-3	same as fluvial
subadult	1-3	1-3	1-3	1-3	same as fluvial

Life history	Temperature (°C)	Age (y)	Biomass (g/m ²)	Abundance (#/100m ²)
Total	< 16	all	5-18	0.3-500
Fluvial				
spawners		3-6		
fry		0		
juvenile	7-16	1-3		0.3-122
subadult		3+		0.2-7
Adfluvial				
spawners		3-6		
fry		0		
juvenile	7-16	1-3		
subadult		3+		
Resident				
spawners		3-5		
fry		0		
juvenile		1-3		
subadult		3+		

Fry emerge after yolk absorption, and at a length of about 20 mm (Shepard et al. 1984). After emergence, many fry disperse downstream. Hoelscher and Bjornn (1989) captured 1,512 trout (cutthroat trout and rainbow trout) fry between 9 June and 5 August in North Fork Grouse Creek, a tributary of Lake Pend Oreille, Idaho. Fry emerged from gravel between 20 June and 14 July. Peaks in the number of

fry moving downstream coincided with peaks in stream discharge.

After an initial exodus of fry, offspring of migratory forms that remain may spend 1-4 years in their natal stream (Block 1955; Johnson 1963; Averett and MacPhee 1971; Rankel 1971; Thurow and Bjornn 1978; Huston et al. 1984; Liknes and Graham 1988). Most emigrants from tributaries of the St. Joe River in Idaho

Table 1.—Continued

Life history	Other fishes in community
Fluvial	
spawners	sculpin, mountain whitefish, bull trout, brook trout, steelhead, hatchery rainbow trout, chinook salmon
fry	sculpin, mountain whitefish, bull trout, brook trout, steelhead, hatchery rainbow trout, chinook salmon
juvenile	northern squawfish, mountain whitefish, brook trout, steelhead, rainbow trout, chinook salmon, cyprinids
subadult	northern squawfish, mountain whitefish, brook trout, steelhead, rainbow trout, chinook salmon, cyprinids
Adfluvial	
spawners	for all life stages, same as fluvial, plus lake species:
fry	kokanee, lake trout, brown trout, cyprinids, northern pike,
juvenile	bass, yellow perch
subadult	
Resident	
spawners	for all life stages: sculpin, bull trout, brook trout,
fry	steelhead, hatchery rainbow trout
juvenile	
subadult	

Table 2.—Maturity rates (proportion mature at age) of westslope cutthroat trout. Data for Hungry Horse Creek, St. Joe River, and Wolf Lodge Creek were summarized by Lukens (1978) and are predicted rates from age composition of spawners. Data for the Coeur d'Alene River (Lewynsky 1986; Apperson et al. 1988) and Middle Fork Salmon River (Mallet 1963) are actual proportions of maturing fish in population samples. Table was adapted from Rieman and Apperson (1989).

Population	Age 3	Age 4	Age 5	Age 6
Hungry Horse Creek	0.10	0.73	0.98	—
St. Joe River	0.18	0.88	0.98	—
Wolf Lodge Creek	0.00	0.03	0.65	0.90
Middle Fork Salmon River	—	0.75	1.00	0.00
Coeur d'Alene River ^a	0.13	0.14	0.60	1.00
Coeur d'Alene River ^b	0.20	0.55	1.00	—

^a Lewynsky (1986).

^b Apperson et al. (1988).

and from Hungry Horse Creek in Montana were age 1 (table 3). As many as 49% of these migrants from Young Creek to Lake Koocanusa, Montana, survived to return as spawners (Huston et al. 1984). Only 28% of adult fish examined in the St. Joe River, however, had immigrated at age 1 (Averett 1962), suggesting that older migrants may have better survival to maturity than do younger ones. Most juvenile migrants leave tributaries in spring or early summer, and most movement is at night (Huston et al. 1984). Some systems may have a fall migration (Liknes 1984). Size of migrants may depend on environment (table 4). Juvenile migrants obtained in sporadic sampling in tributaries of Hayden Lake, Idaho, from April to June were from 94 to 158 mm long (Gamblin 1988). Migrants from a St. Joe River tributary in Idaho cap-

Table 3.—Age distribution of migrant westslope cutthroat trout from tributaries of the St. Joe River, Idaho (Thurrow and Bjornn 1978), Hungry Horse Creek, Montana (Huston 1973), and Young Creek, Montana (Huston et al. 1984).

Location	Number	Age		
		1	2	3
St. Joe River	141	25%	74%	1%
Hungry Horse Creek	563	37%	53%	10%
Young Creek	7168	13%	54%	33%

tured from 5 to 29 June were mostly from 100 to 170 mm long (Thurrow and Bjornn 1978).

Subadult and adult fluvial westslope cutthroat trout (greater than 150 mm) often make long seasonal migrations, e.g., as much as 100 km or more (Bjornn and Mallet 1964; Thurrow and Bjornn 1978; Liknes 1984). Tagged fish in the St. Joe River, Idaho, moved downstream in the fall and back upstream in the spring with little movement in the summer (Thurrow and Bjornn 1978). Most downstream migrants moved at night and after the water temperature had declined below about 15°C. Such migrations presumably are to find areas of suitable winter habitat (Lewynsky 1986; Peters 1988). Little or no movement was observed in systems with an abundance of high quality pools that could be used for winter habitat (Mauser 1972; Peters 1988).

Habitat Relations

Waters inhabited by westslope cutthroat trout generally are cold and nutrient poor (Liknes and Gra-

Table 4.—Estimated mean length-at-age (in mm) for fluvial and adfluvial westslope cutthroat trout. Table was adapted from Rieman and Apperson (1989). Data were summarized by Lukens (1978) and Pratt (1985).

Life history Water	Age						
	1	2	3	4	5	6	7
Fluvial (river)							
Middle Fork Salmon River	60	100	174	254	322	371	
Flathead River	55	103	157	242	305	336	381
Coeur d'Alene River	74	115	175	270	350	420	
St. Joe River	52	91	143	192	243	291	
Marble Creek	50	133	178	235	254		
Kelly Creek	66	101	153	212	251	306	
Adfluvial (lake)							
Wolf Lodge Creek ^a	74	125	214	287	328	365	
Wolf Lodge Creek ^b	69	107	149	236	299	343	
St. Joe River	72	143	266	338	386		
Flathead River	64	120	189	261	311	350	382
Lake Pend Oreille	80	148	261	358			
Priest Lake ^a	89	147	271	326	366		

^a 2-year migrants.

^b 3-year migrants.

ham 1988; Rieman and Apperson 1989). Growth varies widely but is probably strongly influenced by habitat productivity. Growth is generally higher for migrant forms that spend some period in the larger rivers or lakes (Rieman and Apperson 1989).

Although westslope cutthroat trout may be found throughout large river basins, spawning and early rearing occurs mostly in headwater streams (Platts 1979; Rieman and Apperson 1989; Mullan et al. 1992). Spawning habitat has been characterized as gravel substrates with particle sizes ranging from 2 to 75 mm, mean depths ranging from 17 to 20 cm, and mean velocities between 0.3 and 0.4 m/s (Liknes 1984; Shepard et al. 1984). Redds are 0.6 to 1.0 m long and 0.32 to 0.45 m wide (Liknes 1984).

Substrate composition is believed to strongly influence survival. Weaver and Fraley (1991) demonstrated a negative relation between emergence success and the percentage of fine sediment in artificial substrate. Others report that sediment reduces embryo survival (Irving and Bjornn 1984) and food and space for rearing juveniles (Bjornn et al. 1977). Highly embedded substrates may be particularly harmful for juvenile cutthroat trout that typically enter the substrate for cover in winter. Accurately predicting the effects of fine sediment on wild populations remains difficult (Everest et al. 1987; Chapman 1988), and some populations persist despite abundant sediment (Magee 1993). Evidence for a negative influence of fine sediment concentrations is widespread,

however, and in general increased sediment in substrates must be viewed as an increased risk for any population.

Often westslope cutthroat trout are widely distributed in occupied basins (Miller 1957; Platts 1979; Shepard et al. 1984) and may occur in virtually every stream with suitable habitat. Densities may vary widely, however, among streams (Rieman and Apperson 1989; Ireland 1993). Cutthroat trout microhabitats are associated with water velocities ranging from 0.1 to 0.3 m/s (Griffith 1970; Pratt 1984a). Westslope cutthroat trout less than 100 mm long are found predominantly in pools and runs. The distribution and abundance of larger westslope cutthroat trout has been strongly associated with pools (Shepard 1983; Pratt 1984a; Peters 1988; Ireland 1993) and in general stream reaches with numerous pools support the highest densities of fish (Shepard 1983; Peters 1988; Hoelscher and Bjornn 1989; Ireland 1993). Habitats that provide some form of cover also seem to be preferred over those that do not (Griffith 1970; Pratt 1984a; Lider 1985). Fraley and Graham (1981) found the best models for predicting the distribution of trout in the Flathead Basin included cover as an independent variable. In winter, small fish tend to use areas where cover is provided by the interstitial space in the substrate (Wilson et al. 1987; Peters 1988) hence the concern about sediment and embedded substrates. Larger fish congregate in pools during winter (Peters 1988), often in very large numbers (Lewynsky 1986).

It is not clear how strongly variability among local habitats influences the characteristics and dynamics of westslope cutthroat trout populations. A tendency to home to natal streams for reproduction must result in some isolation among groups or subpopulations. A logical consequence of this behavior is that natural selection should tend to produce adaptations to local environments (Leary et al. 1985). No systematic study of the character of site-specific adaptations has been completed for westslope cutthroat trout, but they are thought to be adapted to the presence of a parasite that is indigenous to waters of Glacier National Park (Marnell 1988). Other indirect evidence of local adaptation is the observation that other subspecies of cutthroat trout sometimes do not grow and survive as well as westslope cutthroat trout when they are planted in its habitats (Heimer 1970; Beach 1971; Goodnight and Mauser 1974; Rieman and Apperson 1989).

The relations between salmonid fishes and their habitats have been considered predominantly at the reach, channel unit, and microhabitat scales. Very little is known about habitat relations at larger scales. The potential for separate breeding groups among tributaries suggests that populations exist as part of a larger regional population. The collection of subpopulations within a population is consistent with the concept of a metapopulation (Hanski and Gilpin 1991). Emerging metapopulation theory suggests that the spatial distribution of local populations within a heterogeneous environment may have an important influence on long-term persistence. If populations are not exposed to the same risks, their extinction at the same time is unlikely. The connection of local populations through dispersal is critical to metapopulation dynamics (Hanski and Gilpin 1991; Shaffer 1991; Sjögren 1991). The complexity in such structure provides a species with a mechanism for spreading the risk of extinction (den Boer 1968).

Biotic Interactions

Westslope cutthroat trout coevolved with mountain and pygmy whitefish, several sculpins, cyprinids, and catostomids. In Columbia River tributaries, the subspecies is most commonly associated with bull trout, resident and anadromous rainbow trout or steelhead, and chinook salmon.

Although closely related, cutthroat trout and rainbow trout have remained reproductively distinct where they evolved in sympatry (Behnke 1992).

Where nonnative rainbow trout have been introduced, the species may segregate with rainbow trout in downstream reaches and cutthroat trout in upstream reaches (Hoelscher and Bjornn 1989). Segregation from introduced rainbow trout has been incomplete, however, and hybridization is widespread (Behnke and Zarn 1976; Rieman and Apperson 1989). Hybrids have been identified in the zone of overlap in their distributions (Hoelscher and Bjornn 1989) but are also found throughout much of the range of westslope cutthroat trout where introduced rainbow trout populations are not necessarily strong (Liknes 1984; Rieman and Apperson 1989).

Yellowstone cutthroat trout have also been introduced widely into the range of westslope cutthroat trout (Liknes 1984; Rieman and Apperson 1989). Yellowstone cutthroat trout were often cultured for routine stocking and were particularly popular for use in high mountain lakes (Rieman and Apperson 1989). Hybridization between these subspecies is common and again appears to be a problem throughout most of the range of westslope cutthroat trout.

Westslope cutthroat trout do not seem to be as piscivorous as other cutthroat trout or rainbow trout. Behnke (1992) speculated that adoption of a feeding strategy aimed at invertebrates was a cost of coevolving with the highly piscivorous bull trout and northern squawfish. Sympatric populations of bull trout and westslope cutthroat trout appear to selectively segregate in use of habitat and prey (Pratt 1984a; Nakano et al. 1992). Small rainbow trout and cutthroat trout in Lake Koocanusa, Montana, derived approximately 50% of their caloric intake from *Daphnia* spp. (McMullin 1979). In summer the diets of both species were supplemented with terrestrial insects, fish, and aquatic Diptera. As individuals grew, their diets included increasing amounts of fish, but the rainbow trout ate greater amounts than did cutthroat trout.

Brook trout are thought to have replaced many westslope cutthroat trout populations in headwater streams (Behnke 1992), but the mechanism of interaction is not clear (Fausch 1988; Rieman and Apperson 1989). In the laboratory, Griffith (1972) was unable to show that brook trout displaced equal-sized cutthroat trout. Brook trout may have replaced cutthroat trout through some form of competitive displacement or simply filled empty habitat when cutthroat trout declined from some other cause (Griffith 1970, 1988). Cutthroat trout fry did survive better when planted in tributaries of Priest Lake, Idaho,

where brook trout were absent (Cowley 1987; Irving 1987). When the two species coexist, cutthroat trout seem to predominate in the higher gradient reaches (Griffith 1988), whereas brook trout may prevail in lower gradients. Existing data for Idaho and Montana watersheds suggest that westslope cutthroat trout are most abundant in reaches with 6 to 14% gradient and occur in gradients up to 27% (Fausch 1989). Fausch (1989) indicated that brook trout attained greatest abundance at less than 3% gradient and were not found at greater than 15% gradient. Fausch (1989) speculated that brook trout either do not enter or do not survive and reproduce in reaches that exceed 7% gradient. As a result, high-gradient reaches provide refuges for cutthroat trout. He concluded that brook trout probably are not well adapted to life in steep gradients whether or not cutthroat trout are present, and cutthroat trout would be more abundant than has been observed in lower gradient reaches if brook trout were absent.

Feldmuth and Eriksen (1978) conducted experiments to estimate the "critical thermal maximum" (CTM) for westslope cutthroat trout. The CTM was 27.1°C for cutthroat trout, a value lower than those estimated for brook trout (29.8°C), brown trout (29.6°C), and rainbow trout (31.6°C). Native cutthroat trout are apparently less tolerant of warm water than are nonnative salmonids. Native cutthroat trout might therefore fare better in interactions with nonnative salmonids in colder waters, but less well in warmer waters (cf. DeStaso and Rahel 1994). Mullan et al. (1992) speculated that water temperature may play an important role in the displacement of native cutthroat trout and bull trout by rainbow trout in tributaries of the Methow River, Washington.

Reasons for Concern

The current distribution and abundance of westslope cutthroat trout appear to be severely restricted compared with historical conditions (Bjornn and Liknes 1986; Liknes and Graham 1988; Rieman and Apperson 1989; Behnke 1992). Declines are probably continuing in much of the remaining range. Westslope cutthroat trout are now believed to persist in only 27% of their historical range in Montana, and are genetically unaltered in only 2.5% of the native range (Liknes 1984; Liknes and Graham 1988). Rieman and Apperson (1989) estimated that populations considered as "strong" (greater than or equal to 50% of historical potential) by Idaho Department

of Fish and Game biologists remained in only 11% of the historical range. Idaho biologists also believed that less than 4% of the historical range supported strong populations not threatened by hybridization (Rieman and Apperson 1989).

Construction of dams, irrigation diversions, or other migration barriers such as culverts (Rieman and Apperson 1989) have isolated or eliminated areas of westslope cutthroat trout habitat that were once available to migratory populations. There has been no effort to quantify the amount of habitat lost, but whole river basins have been blocked (e.g., Pend Oreille River, South Fork Flathead River). Resident forms may persist in isolated segments of streams, but the loss of the migratory life history and the connection with other populations potentially important to gene flow or metapopulation dynamics may seriously compromise the potential for long-term persistence.

Climate change may play an important role in the further restriction of westslope cutthroat trout populations in the future. Westslope cutthroat trout appear to prefer colder water than do other salmonids. The primary distribution of rearing populations is often in the upper, cooler reaches of drainage basins. Mullan et al. (1992) speculated that warmer temperatures associated with climate change would result in further restriction of cutthroat trout in the Methow River basin. Neitzel et al. (1991) summarized available models of climate change, suggested that mean air temperatures in the Pacific Northwest may increase by 2°C to 5°C in the next 50 to 100 years, and inferred catastrophic effects for many salmon stocks. Kelehar and Rahel (1992) used a similar approach to predict that the current range of cutthroat trout in Wyoming would decline by 65% with a 3°C warming in summer air temperature. An equally severe restriction in distribution might also be expected in the range of westslope cutthroat trout in Idaho and Montana.

Fragmentation of habitats and the consequent isolation of local populations may threaten the persistence of many species (Gilpin and Soulé 1986; Hanski and Gilpin 1991; Sjögren 1991; Rieman et al. 1993). Isolation of cutthroat trout populations has resulted from human-caused habitat and environmental changes. Overfishing and competition also restrict their distribution to a smaller portion of the original range. Populations have been reduced in abundance and an increasing number are being isolated from other populations (Rieman and Apperson 1989).

The probability that a local population will persist depends on the quality of its habitat, but perhaps also

on chance events and the connections to other populations. In general, managing cutthroat trout has focused on preserving good habitat wherever it remains. Although biologists generally have some sense of what good habitat is and how to protect it, relatively little is known about the appropriate amount or distribution of habitat necessary to ensure long-term persistence. A growing body of both theoretical and empirical work indicates that the persistence of many species will be strongly dependent on both the amount and spatial geometry (or isolation) of available habitat (see Rieman et al. 1993). Viability analyses have been conducted for many species both to quantify extinction risks and to evaluate the design of conservation reserves. Such analyses generally require extensive data that are unavailable for most westslope cutthroat trout populations. It is still useful, however, to consider the processes of extinction and the nature of the risks relevant for many cutthroat trout populations.

Extinction risks for a species might be characterized as deterministic, genetic, or stochastic (Leigh 1981; Gilpin and Soulé 1986). Deterministic risks include cumulative effects that result in mortality that cannot be compensated by increased survival at another stage. For example, increased fishing and cumulative habitat degradation have led to increased mortality in westslope cutthroat trout populations (Bjornn et al. 1977; Weaver and Fraley 1991) and may be responsible for the disappearance of many populations (Rieman and Apperson 1989). The regional declines in abundance and continuing loss of populations indicate that deterministic risks are high for westslope cutthroat trout through much of its range.

Genetic risks include loss of genetic variation through reduction in population size and loss of genetic integrity through hybridization with introduced species (Allendorf and Phelps 1980; Leary et al. 1984; Allendorf and Leary 1988). Hybridization has been widely recognized, and the loss of variation is becoming better known (Liknes 1984; Liknes and Graham 1988). Loss of variation and fitness through small population size has been demonstrated in hatchery stocks of westslope cutthroat trout (Allendorf and Phelps 1980) and in hybridized populations of other salmonids (Leary et al. 1985). The effects of small population size have not been demonstrated in situ (R. Leary, University of Montana, pers. commun.). Nevertheless, loss of genetic variation must be considered a long-term risk in isolated or severely restricted populations of any species (Soulé

1980; Gilpin and Soulé 1986). In the short term, however, many populations likely face greater risks from deterministic and stochastic effects than from loss of genetic variation associated with restricted population size (Shaffer 1987; Stacey and Taper 1992).

Stochastic risks are associated with chance events. They have been characterized as demographic and environmental (Leigh 1981; Shaffer 1987, 1991; Ginzburg et al. 1990). Demographic stochasticity includes the random variation in individual birth, death, reproduction, or other characteristics even though the underlying rates may be stable. In general, demographic effects for most species will be felt only at very small (i.e., fewer than 20 to 50 adults) population sizes (Leigh 1981; Shaffer and Sampson 1985; Gilpin and Soulé 1986; Quinn and Hastings 1987; Shaffer 1987). Environmental stochasticity includes random variation in mortality and birth rates driven by environmental variation and is potentially more important than is demographic stochasticity (Shaffer 1987). Risks related to random variation may be high for many species (Leigh 1981; Gilpin and Soulé 1986; Shaffer 1987; Dennis et al. 1991) but generally have not been considered for salmonids.

Dennis et al. (1991) developed an analytic estimation method for extinction parameters based on time series data of population sizes. In essence the probability of a population dropping below some critical number within some period of time can be estimated from information on the variability in number, the initial size of the population, and any trend in population growth. We used the methods of Dennis et al. (1991) to approximate such risks for small populations of westslope cutthroat trout.

We used sequential population density estimates from several streams to estimate variance in the rate of population growth (table 5) as described by Dennis et al. (1991). An extended time series (more than 5 years) was not available for cutthroat trout populations in the Bitterroot River system so we replicated observations through space rather than time. In substituting space for time we assumed that all populations are representative of a single population and that the annual transitions are independent among populations. Those assumptions may be inappropriate in the strictest interpretation, but we believe they are still useful for a first approximation of variation possible in these populations. Violation of our assumptions will most likely lead to an underestimate of the true variances, because of the limited time scale (Pimm and Redfearn 1988) and the potential for spa-

Table 5.—Estimated variance in the infinitesimal rate of growth for westslope cutthroat trout populations monitored in Idaho and Montana. The 95% confidence interval is shown in parentheses. Estimates are calculated after Dennis et al. (1991).

Stream State	Years	Variance	Source
Bitterroot River, ^a Montana	22	0.29 (0.19–0.52)	C. Clancy, Montana Dept. Fish, Wildlife and Parks, pers. commun.
Young Creek, Montana	11	0.3 (0.16–0.78)	Huston et al. (1984)
North Coal Creek, Montana	10	0.11 (0.06–0.29)	Weaver (1992)
South Coal Creek, Montana	6	0.2 (0.09–0.88)	Weaver (1992)
Middle Fork Salmon River, Idaho	7	1.02 (0.49–3.78)	Liter and Lukens (1992)
Lochsa River, Idaho	7	0.69 (0.31–3.01)	Lindland (1982)
St. Joe River, Idaho	10	0.07 (0.04–0.21)	T.C. Bjornn, University of Idaho, pers. commun.

^a Transitions from 12 streams monitored over 2 to 3 years were pooled as a single population.

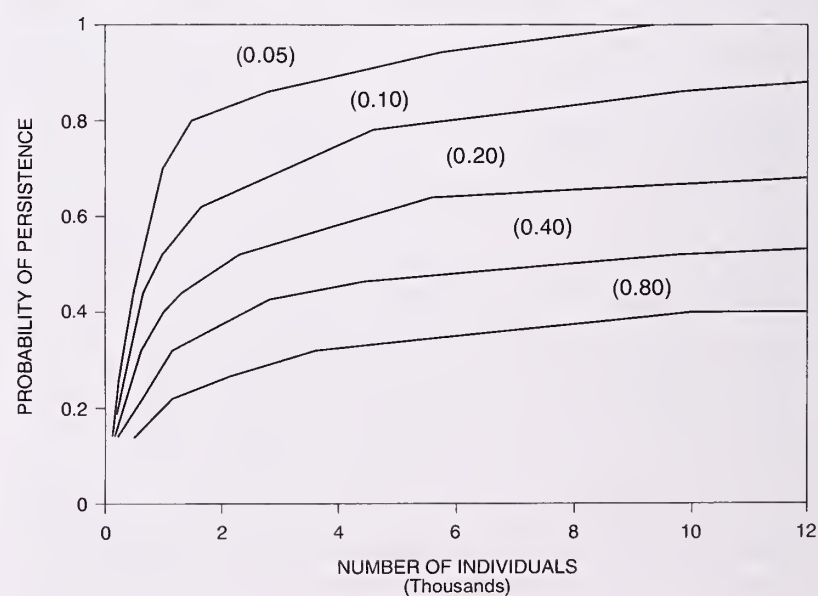
tial autocorrelation among populations within years. We considered the annual transitions observed over 3 years within 12 headwater streams to be suitable, although probably conservative estimates of the transitions expected in one system over a longer time.

We estimated the probability of persistence above a threshold of 100 individuals in a population for 100 years. From existing work it appears that adult fish probably represent 20% or fewer of total individuals in most populations (Johnson and Bjornn 1978; Liter and Lukens 1992). We assumed then that 100 total individuals represented an adult population size of fewer than 20, a point short of complete extinction, but certainly low enough to result in serious risk from other factors, i.e., genetic and demographic (Dennis et al. 1991). We did not estimate the mean annual growth rate for populations (Dennis et al. 1991), but rather assumed that all populations varied around some equilibrium with no long-term trend of growth or decline. Our results therefore represent the risks associated with random and not deterministic effects.

The estimated variances for the annual growth rates ranged from 0.07 to about 1.0 (table 5). Estimates were relatively imprecise because of small sample sizes, but provide some indication of the relative stability expected in westslope cutthroat trout populations over a range of sites. The data suggest that variances less than 0.05 are unlikely but substantially higher values are possible, considering our conservative estimates. General predictions of persistence above the threshold were strongly influenced by both the variance and initial population size (figure 1).

If the estimated variances are representative, the results indicate that stochastic risks will increase quickly for many populations that drop to fewer than 2,000 individuals. Any habitat condition or environmental variation that resulted in population variances comparable to the higher estimates used here would also result in high risks. Hunt and Bjornn (1992) estimated that only 800 cutthroat trout remained in the North Fork Coeur d'Alene River. Extrapolations of population density estimates to available habitat suggest that some populations in tribu-

Figure 1.—Estimated probabilities of persistence for 100 years for populations of different initial size and temporal variance in instantaneous rate of growth. Variances are shown in parentheses. Calculations are after Dennis et al. (1991). The threshold of persistence was assumed to be 100 individuals.



taries to the Bitterroot River number from 1,000 to 2,000 individuals (C. Clancy, Montana Department of Fish, Wildlife and Parks, pers. commun.). Elsewhere, some isolated populations are even smaller (B. Shepard, Montana Department of Fish, Wildlife and Parks, pers. commun.).

Extinction risks related to random variation of populations appear to be an important cause for concern. Extinction for many isolated populations may simply be a matter of time. Although our estimates are the result of crude approximations, they are consistent with a growing body of evidence for similar risks for many species (see Rieman et al. 1993). Our estimates do not include the potential for catastrophic loss and might therefore be overly optimistic (see Mangel and Tier 1994). If chance events represent an important risk for many populations, further loss of cutthroat trout populations will likely continue even with no further loss of habitat. Effective conservation of the subspecies will probably require the maintenance or restoration of well-connected mosaics of habitat (see Frissell et al. 1993; Rieman et al. 1993; Rieman and McIntyre 1993).

Causes of the Decline

Causes of the decline of westslope cutthroat trout include competition with and predation by non-native species, genetic introgression, overfishing, habitat loss and fragmentation, and habitat degradation (Liknes 1984; Liknes and Graham 1988; Rieman and Apperson 1989). Habitat loss was identified as the primary cause of decline in 87% of the stream reaches supporting depressed populations in Idaho (Rieman and Apperson 1989). Fishing contributed to the decline in 47% of the reaches. Competition and genetic introgression were considered to be important causes for decline in 12% and 15%. Genetic introgression was believed to be the most important cause for decline of westslope cutthroat trout populations in Montana (Liknes and Graham 1988).

Nonnative salmonids have been planted throughout the range of westslope cutthroat trout including Glacier National Park (Marnell 1988). Behnke (1992) speculated that nonnative species such as kokanee, lake trout, and lake whitefish caused declines of westslope cutthroat trout in lakes. Predation and competition are both thought to be important. Opossum shrimp (*Mysis relicta*) have also been introduced in several lakes in Idaho and Montana and might influence cutthroat trout populations as well. As

westslope cutthroat trout declined in several locations, planted kokanee populations increased, but it is not clear whether the trends are circumstantial or reflect an important interaction. Some westslope cutthroat trout populations have persisted despite the presence of large kokanee populations (Rieman and Apperson 1989).

Fausch (1988,1989) concluded that the persistence of westslope cutthroat trout is jeopardized in streams also supporting brook trout or brown trout. Behnke (1992) concluded that brown trout, brook trout, and rainbow trout, along with changes in flow and water quality, were responsible for the demise of westslope cutthroat trout in the Spokane and Clark Fork drainages.

Westslope cutthroat trout have been identified in stomachs of bull trout, lake trout, and sculpins (Beach 1971; Athearn 1973; Mauser 1986). Predation clearly happens, but the relative importance of such predation in the decline of westslope cutthroat trout has not been identified. Jeppson and Platts (1959) and MacPhee and Reid (1971) reported increased survival of cutthroat trout following intensive removal of northern squawfish, but others have found little evidence that such predation was important (Bjornn 1957; Jeppson 1960; Falter 1969; Apperson et al. 1988). Rieman and Apperson (1989) argued that predation, especially in combination with fishing, can act as a compensatory source of mortality and maintain a population in a low equilibrium region compared with historical levels (see Peterman 1977). The importance of such a predator trap for westslope cutthroat trout, however, is yet to be demonstrated.

Westslope cutthroat trout are highly susceptible to angling (MacPhee 1966; Lewynsky 1986; Behnke 1992). Population abundance and average body size have increased in several populations following angling restrictions (Johnson and Bjornn 1978; Thurow and Bjornn 1978; Peters 1988; Rieman and Apperson 1989). Rieman and Apperson (1989) found evidence of a compensatory effect in fishing (mortality increases with decline in population size) and speculated that harvest could lead to the elimination of some small populations. Others believe that angling pressure led to the virtual elimination of fluvial fish in some river systems (T.C. Bjornn, University of Idaho, pers. commun.). Special harvest restrictions may be necessary to maintain most westslope cutthroat trout populations (Rieman and Apperson 1989).

Despite the obvious influence of fishing, its importance relative to other causes of decline is not clear.

The westslope cutthroat trout in the Coeur d'Alene River, for example, did not respond to special regulations, perhaps because of noncompliance with angling regulations, harvest during other portions of the life history, or stress caused by catch-and-release angling (Rieman and Apperson 1989). Fishery managers speculated that degraded habitat prevented any population response (N. Horner, Idaho Department of Fish and Game, pers. commun.). Fishing has clearly caused the decline of the older and larger members of some populations and may ultimately limit recruitment. Thurow and Bjornn (1978) reported greater densities of cutthroat trout fry in stream reaches closed to fishing and concluded that fishing may have limited fry recruitment in other unregulated reaches.

Habitat loss and degradation are primary concerns of many biologists working with westslope cutthroat trout (Liknes 1984; Liknes and Graham 1988; Rieman and Apperson 1989). Forest management has probably played an important role in habitat disruption but its effects are not always consistent or easily predictable. Increased fine sediment has generally been a primary concern of biologists dealing with fish habitat relations (e.g., Stowell et al. 1983; Rieman and Apperson 1989). The number of salmonids, including westslope cutthroat trout, observed in snorkeling surveys in the South Fork Salmon River, Idaho, was negatively correlated with measures of substrate embeddedness (Thurow 1987); other work predicted a substantial reduction in incubation or emergence survival with increased fine sediment (Irving and Bjornn 1984; Weaver and Fraley 1991). Westslope cutthroat trout abundance, however, could not be clearly associated with intragravel fine sediment in Idaho's Coeur d'Alene River (Gamblin 1988) or in tributaries to the Bitterroot River, Montana (Clancy 1993). Much of the area where westslope cutthroat trout are located is in belt geologies where roads and timber harvest seem to aggravate problems associated with coarse (50–150 mm) rather than with fine substrates (Gamblin 1988; Rieman and Apperson 1989; G. Kappesser, Idaho Panhandle National Forests, pers. commun.). In many watersheds excessive bedload transport and scour are obvious problems during peak flows (G. Kappesser, Idaho Panhandle National Forests, pers. commun.). In low-gradient reaches bed aggradation may result in the loss of pools, reduced pool volume, and channel dewatering during low flows. The relatively simple and unstable channels that result from intensive manage-

ment of these basins were overlooked as problems in earlier concerns focused on fine sediment (Gamblin 1988; Rieman and Apperson 1989). It is evident now, however, that intensive management may lead to habitat disruption through a variety of mechanisms.

Disturbance of stream banks and riparian areas, construction of roads, and removal of upland vegetation have been associated with alteration of stream flows, increased erosion and sediment loading, and increased temperatures. There is a large body of information documenting the effects of such disturbance on habitat for stream salmonids (e.g., Brown and Krygier 1970; Salo and Cundy 1987; Meehan 1991). The nature and magnitude of channel and habitat changes may vary with the type, extent, and intensity of disturbance, with the species involved, and with physiographic characteristics of the watershed. Often it has proven difficult to quantify or predict effects precisely. The results of existing studies do not permit clear conclusions regarding causes or the magnitude of population declines. It is clear, however, that habitat disruption can result from intensive forest management, and that such changes can directly influence populations in negative ways.

The causes for decline of westslope cutthroat trout are no doubt varied. That most strong populations remain largely in roadless and wilderness areas or national parks (Liknes 1984; Liknes and Graham 1988; Marnell 1988; Rieman and Apperson 1989), however, is clear evidence that human intervention has been important.

Current Management

Westslope cutthroat trout are considered sensitive by Regions 1 and 4 of the USDA Forest Service and by the USDI Bureau of Land Management, and considered a species of special concern by the Idaho Department of Fish and Game (Moseley and Groves 1990). The Idaho Department of Fish and Game has made extensive use of restrictive fishing regulations (e.g., size limits, reduced bag limits, catch and release, closures) in most systems supporting westslope cutthroat trout populations (Rieman and Apperson 1989). The Montana Department of Fish, Wildlife, and Parks has undertaken extensive habitat restoration (Rieman and Apperson 1989) and instituted a system of protective harvest regulations (Liknes 1984). Both states have established captive broodstocks free of introgression from rainbow trout or Yellowstone

cutthroat trout. In Montana, stocking has been used to restore westslope cutthroat trout populations in waters where they once occurred but have been either eliminated or introgressed with nonnative trout. Westslope cutthroat trout are now stocked in place of other trout in Idaho mountain lakes within the subspecies' range. Net pen and hatchery rearing are also used to supplement or support fisheries for westslope cutthroat trout in Idaho where wild populations are believed to be nonviable, where they have been displaced by other species, or where hybridization with other subspecies of cutthroat trout or rainbow trout has been extensive (Rieman and Apperson 1989). The range of westslope cutthroat trout in Idaho has been reduced to such an extent that the remaining populations are considered extremely important (Rieman and Apperson 1989).

Research Needs

Interactions with nonnative species through predation, competition, or hybridization are believed to be an important threat. The risks and magnitude of displacement are poorly understood. It is not clear whether displacement by nonnative species is inevitable throughout the range or whether some populations are at much greater risk than others. It is not clear how habitat disruption or other human effects may aggravate the risks.

Westslope cutthroat trout populations are becoming increasingly fragmented and isolated. New work should describe risks associated with small population size and isolation. Emerging metapopulation theories may apply to trout populations, but there is little information to validate this. New work considering larger scale spatial patterns in habitat and fish distribution, dispersal rates and mechanisms, and disturbance regimes is needed.

The spatial and temporal distribution of each life-stage of westslope cutthroat trout is not well documented. Habitat preferences or requirements are suspected, but not well defined. More effective measures of habitat quality or suitability are needed to improve recognition of important habitat disruption. Such measures would also help identify the most productive or highest potential areas for long-term conservation.

Life history diversity is suspected to be an important mechanism for stabilizing populations in highly variable environments and may play an important role in the long-term persistence of cutthroat trout

populations. The relation between resident and migratory forms and the differences in habitat requirements or sensitivity to habitat disruption should be better defined.

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Chapter 2

Colorado River Cutthroat Trout

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Introduction

The Colorado River cutthroat trout historically occupied portions of the Colorado River drainage in Wyoming, Colorado, Utah, Arizona, and New Mexico (Behnke 1992). Though it is now restricted to headwater streams and lakes, its original distribution probably included portions of larger streams, such as the Green (Simon 1935), Yampa, White, Colorado, and San Juan rivers.

Behnke and Zarn (1976) speculated that this subspecies was absent from the lower reaches of many large rivers because of thermal barriers in summer. Yet other subspecies of cutthroat trout have seasonally migrated over 100 km, usually upstream in spring and downstream in autumn (Bjornn and Mallet 1964). Similarly, in late fall brown trout have moved over 35 km to habitats considered marginal in summer (Meyers et al. 1992). Thus portions of these lower reaches may have become acceptable in winter as water temperatures moderated and may partially explain the apparently disjunct historical distribution of this subspecies.

Life History Characteristics

The diversity of life histories exhibited by this subspecies has probably been reduced. Adfluvial stocks may have occupied a number of high-elevation lakes (e.g., on the southwestern slope of the Wind River Range in Wyoming [Simon 1935] or on the west slope of the Park Range in Colorado), but these stocks have been largely eliminated. Most remaining populations are fluvial or resident, though reestablished lacustrine stocks of Colorado River cutthroat trout have been reported in Wyoming (R. Remmick, Wyoming Game and Fish Department, pers. commun.) and Rocky Mountain National Park in Colorado.

Spawning by this subspecies begins after flows have peaked in spring or early summer and ends before runoff subsides (Quinlan 1980; Young, pers. obs.). Water temperature may also act as a cue for the timing of spawning (Quinlan 1980). In tributaries of the North Fork Little Snake River, Wyoming, adults returned to the mainstem shortly after spawning (Young, unpubl. data). In contrast, many spawning fish remained in tributaries of Trappers Lake, Colorado, after late July (Snyder and Tanner 1960). Fluvial Colorado River cutthroat trout have spawned in intermittent streams that were unsuitable adult habitat (Jespersen 1981; cf. Erman and Hawthorne 1976). In Trappers Lake, 16% of the spawning run consisted of repeat spawners, and most had spawned the previous year (Snyder and Tanner 1960), but the proportion and frequency of repeat spawning in fluvial or resident populations is unknown.

The fecundity of Colorado River cutthroat trout presumably varies with length, location, and life history. Based on 13 trout from 149 to 210 mm from Solomon Creek, Wyoming, Quinlan (1980) related total length in mm (x) to egg number (y) by using the equation $y = -266.56 + 2.63(x)$. Fecundity of 16 females (mean length 290 mm) from a tributary to Trappers Lake was 667 eggs (Snyder and Tanner 1960).

Water temperature, influenced by elevation and annual climatic variation, controls the time of emergence, which tends to be in late summer in streams still containing this subspecies. Near 2,700 m above mean sea level in Wyoming, Jespersen (1981) first found swim-up fry in late August, but also found alevins in the substrate as late as early September. At 2,708 m above mean sea level in Colorado, Scarnecchia and Bergersen (1986) observed emerging fry in late July and early August, as did Snyder and Tanner (1960) and Drummond (1966) in tributaries of

Trappers Lake near 2,950 m above mean sea level. In these tributaries, most fry began migrating to the lake shortly after emergence, and migration continued through mid-September, though some fry were thought to remain in the tributaries over winter (Snyder and Tanner 1960).

Length and age at maturity are related to food abundance and the length of the growing season. Colorado River cutthroat trout reached maturity at age 3 and averaged 146 mm in the North Fork Little Snake River drainage; no fish were older than age 6 (as aged by scales), and few were over 200 mm (Quinlan 1980). In the same watershed, Jespersen (1981) found no fish larger than 250 mm, and he estimated abundances from 77 to 609 fish/km and biomasses from 3.1 to 109.4 kg/ha. Growth rates in this stream were one-third to one-half those reported for cutthroat trout elsewhere in the western United States (Bozek et al. 1994). Similarly, the largest Colorado River cutthroat trout observed in Little Green Creek, Colorado, was 202 mm (Scarnecchia and Bergersen 1986). They also noted that production and the production:biomass ratio of Colorado River cutthroat trout were among the lowest reported for salmonids, which they attributed to the short growing season at high elevations.

Nevertheless, this subspecies can reach larger sizes. Fish less than 200 mm (from the North Fork Little Snake River drainage) were transplanted to a lower-elevation pond and reached 380 mm after 2 years (M. Fowden, Wyoming Game and Fish Department, pers. commun.). Remmick (no date) reported that this subspecies commonly exceeded 254 mm and reached 335 mm in tributaries of the Green River, Wyoming, especially those streams with beaver ponds. In contrast, lake-dwelling Colorado River cutthroat trout averaged 325 mm at age 3 (Drummond 1966), and older fish occasionally surpassed 470 mm (Colborn 1966). Behnke (1992) cited unconfirmed historical accounts of this subspecies reaching 10 kg west of the Continental Divide in Colorado.

Habitat Relations

The seasonal habitat requirements of various life stages of Colorado River cutthroat trout have rarely been studied, and then largely in summer. For example, Binns (1977) provides information on water quality and habitat from 13 streams in Wyoming, but conclusions were based on a single visit to each stream between July and October from 1968 to 1975.

Typical of most Salmoninae, Colorado River cutthroat trout spawn in substrate predominantly composed of gravel. The mean dominant particle size in 34 redds in the North Fork Little Snake River drainage was 30 mm (Jespersen and Conder 1986). The geometric mean particle size of 41 redds in the North Fork Little Snake River drainage averaged 10.4 mm and ranged from 3.7 to 22.8 mm (Young 1989). Laboratory studies revealed that geometric mean particle sizes from 13.8 to 15.9 or larger yielded the best survival (Young et al. 1991).

Redds tend to be located where velocity, depth, and bottom configuration induce water flow through the stream substrate (Young 1989). Jespersen and Conder (1986) measured a mean depth of 18 cm and a mean nose velocity of 34 cm/s over 34 recently constructed redds in the North Fork Little Snake River watershed. By late summer, flows had declined substantially in the spawning area; 21% of the redds were dry, but fry may have already emerged. Near the time that eggs hatched in 1987, Young (unpubl. data) measured a mean depth of 11 cm and a mean nose velocity of 15 cm/s over 33 redds in that watershed.

Bozek and Rahel (1991a) characterized fry summer microhabitats as sites with water velocities slower than 6 cm/s and in water deeper than 3 cm; woody debris, boulders, and rootwads sheltered these sites from higher water velocities. Yet many reaches with suitable microhabitats contained no fry, and they concluded that the presence of spawning gravel (and thus redds) was requisite for the presence of fry.

The identification of variables important to adults has been inconsistent. Some researchers have electrofished stream reaches (Jespersen 1981) or individual habitat types (Herger 1993) to relate fish abundance to habitat characteristics. A multiple regression equation including spawning habitat, cover, and riffle water velocity as independent variables accounted for 78% of the variation in Colorado River cutthroat trout biomass in the North Fork Little Snake River drainage, and spawning habitat was the single most important variable (Jespersen 1981). Herger (1993) found that most Colorado River cutthroat trout larger than 152 mm were in pools, and that pool depth influenced trout density. Yet cover features were not related to trout abundance, nor was the kind of pool, e.g., plunge pool or dammed pool. Also, the density of fish in pools increased as the flows declined over the summer (Herger 1993).

The repeated location of individual fish with radiotelemetry has yielded different results. Young

(unpubl. data) compared the characteristics of habitats used by and available to adult Colorado River cutthroat trout in the North Fork Little Snake River drainage. Nearly 40% of the habitats occupied by these fish were created by coarse woody debris, yet fewer than 10% of the stream consisted of such sites. Habitats created by meanders were significantly underused. The mean depth of used habitats was significantly greater than that of available sites. Used sites had significantly lower average water velocities near the stream bottom and surface than those available. But there were no significant differences in mean water velocity or in distance to cover between used and available habitats, and fish positions tended to be significantly farther from the banks than would be expected by chance alone.

Low fish densities may further confound interpretations of habitat use. Herger (1993) reported that many apparently suitable pools in the North Fork Little Snake River drainage contained no fish. Quinlan (1980) noted that large pools in the same drainage typically contained one adult Colorado River cutthroat trout and few or no juveniles.

Additionally, fish movement complicates the assessment of habitat use, and the delineation of populations. Research on several cutthroat trout subspecies has suggested that most small-stream inhabitants are residents with short home ranges (e.g., 18 m, Miller 1957; 4 m, Heggenes et al. 1991), but this may have resulted from methodological constraints (Gowan et al., in press). Quinlan (1980) suggested that Colorado River cutthroat trout did not migrate in the North Fork Little Snake River drainage. But Jespersen (1981) noted that stream reaches in different portions of the North Fork Little Snake River watershed contained different age structures of Colorado River cutthroat trout (i.e., smaller fish upstream, larger fish downstream), and Remmick (no date) observed this pattern in tributaries and the main stem of Rock Creek, Wyoming; both considered this evidence of fish movement. Also, Jespersen (1981) captured some juvenile fish that were migrating downstream in late summer and early fall. Young (unpubl. data) found that adult Colorado River cutthroat trout in the North Fork Little Snake River drainage occupied home ranges over 1,000 m from June to mid-August. After spawning and leaving tributaries, adults moved both up- and downstream from tributary mouths. Minimum weekly movement in late June and early July averaged 125 m, but declined to 14 m by mid-August.

Identifying distinct populations may be difficult if fish move to different streams. For example, a single radio-tagged adult occupied Green Timber Creek, Harrison Creek, and the North Fork Little Snake River above and below the mouths of these tributaries within 3 weeks (Young, unpubl. data). Snyder and Tanner (1960) reported that several males marked in one tributary to Trappers Lake were recaptured 4 weeks later in another tributary at the opposite end of the lake. Traditionally, different tributaries were believed to contain discrete populations, but the mobility of fishes makes this view questionable (Fausch and Young, in press). The characteristics of natural barriers to movement that might isolate populations have not been studied, but Snyder and Tanner (1960) suggested that a 100-m reach with a 19.3% gradient blocked spawning migrations, whereas a 17.3% gradient did not.

Biotic Interactions

Colorado River cutthroat trout evolved in sympatry with several other species, but no closely related salmonids. In the Wyoming portion of the North Fork Little Snake River watershed, Colorado River cutthroat trout are sympatric only with mottled sculpin, though they historically shared nearby reaches with flannelmouth sucker, bluehead sucker, mountain sucker, speckled dace, roundtail chub, mountain whitefish (Eiserman 1958), and probably Colorado squawfish (Baxter and Simon 1970). Other portions of the historical range of Colorado River cutthroat trout also contained species of sculpins (Cottidae), suckers (Catostomidae), and minnows (Cyprinidae). The past or current influence of these other species on Colorado River cutthroat trout is unknown. Only anecdotal evidence exists on the influence of other vertebrates, such as predatory birds and mammals or beaver, on this subspecies. For example, dippers (*Cinclus mexicanus*) captured young-of-the-year trout from stream margins in the North Fork Little Snake River (M. Bozek, National Biological Survey, pers. commun.), and mink (*Mustela vison*) preyed on adults in this watershed in late autumn (S. Pearce, Rocky Mountain Forest and Range Experiment Station, pers. commun.).

The diets of Colorado River cutthroat trout have not been comprehensively studied. Colborn (1966) noted that amphipods, other plankton, dipterans, and terrestrial hymenopterans were important components of the summer diet of Colorado River cutthroat

trout in Trappers Lake, Colorado. Small fish were present but rarely eaten. In contrast, adult fish in a tributary to Trappers Lake contained an average of 61 fry (Snyder and Tanner 1960). Bozek et al. (1994) failed to find any young-of-the-year in stomach samples from larger Colorado River cutthroat trout in the North Fork Little Snake River. In streams of the upper Green River drainage, Colorado River cutthroat trout primarily ate dipterans and ephemeropterans, but also consumed most of the available invertebrates (Remmick, no date). In Harrison Creek, Wyoming, a one-day sample revealed that adult Colorado River cutthroat trout ate more large food items and a greater proportion of terrestrial insects than did smaller fish (Bozek et al. 1994). Dipterans constituted the dominant food of all size classes.

The behavior patterns of this subspecies may reveal the relative importance of foraging compared with predator avoidance. Most young-of-the-year trout of this subspecies were visible to observers, and nearly half these fish refused to escape to cover despite disturbance (Bozek and Rahel 1991b). Young (unpubl. data) found that Colorado River cutthroat trout could be seen 75% of the time during the day after being located by radiotelemetry. In contrast, brown trout in nearby streams were only visible 10% of the time once located (Young, unpubl. data). Furthermore, brown trout activity peaked near midnight, whereas the activity of Colorado River cutthroat trout declined at night, but peaked at various times during the day. Moreover, coastal cutthroat trout may choose microhabitats based on food availability rather than on the presence of cover (Wilzbach 1985), possibly because foraging efficiency is influenced by light intensity (Schutz and Northcote 1972; Wilzbach et al. 1986), and this behavior may also apply to Colorado River cutthroat trout. Because their daytime positions are not associated with banks or overhead cover, Colorado River cutthroat trout may be risking greater predation to focus on daytime foraging.

Very little is known about the diseases and parasites of this subspecies. In the North Fork Little Snake River drainage, *Gyrodactylus* is present and may cause death of severely stressed fish (Jespersen 1981). Other data are not available.

Reasons for Concern

The abundance and distribution of Colorado River cutthroat trout have declined so much since the arrival of Europeans that calls have been made for fed-

eral listing (Behnke and Zarn 1976). Behnke (1979) stated that the Colorado River cutthroat trout occupied less than 1% of its historical range. Martinez (1988) reported that of 37 populations in northwestern Colorado sampled from 1978 to 1987, 12 apparently declined in genetic purity, 3 were replaced by populations of brook trout, and 1 population disappeared, possibly because of overharvest. By 1977, Colorado River cutthroat trout in Wyoming were thought to be restricted to 40 streams and 2 lakes, and only 8 of these populations were regarded as genetically pure, based on meristic analyses (Binns 1977). Furthermore, most lotic populations were in isolated, headwater streams with average daily flows less than 0.85 m³/s and often less than 0.14 m³/s. Stream gradients usually exceeded 4%, and all fish were found above 2,290 m. Based on samples from 17 Wyoming streams, Oberholtzer (1990) estimated that there were 52 adult Colorado River cutthroat trout per km of stream.

Other concerns include the loss of novel stocks and the fragmentation of habitats. Most adfluvial stocks have been lost, though some are being reestablished in lakes in Rocky Mountain National Park from a population stocked in the Williamson lakes, California, in 1931 (Pister 1990). Most streams in the North Fork Little Snake River watershed that contain Colorado River cutthroat trout have been fragmented by the installation of water diversion structures that limit up- and downstream fish passage (Oberholtzer 1990). Streams in other watersheds often have populations of nonnative salmonids in lower reaches that seemingly prevent recolonization by Colorado River cutthroat trout.

Causes of the Decline

Introductions of nonnative salmonids may have had the greatest effect on Colorado River cutthroat trout. Stocking of these nonnative salmonids has been widespread since before 1900, and records of many introductions do not exist. More recent records for the North Fork Little Snake River drainage suggest that rainbow trout were first introduced in 1950 and Yellowstone cutthroat trout and brook trout in 1936 (Oberholtzer 1987). In the Savery Creek drainage, tributary to the Little Snake River, rainbow, brook, and brown trout were first introduced in 1936 and fine-spotted or Yellowstone cutthroat trout possibly were introduced in 1933 (Eiserman 1958). Rainbow trout were first stocked in 1915 in the Smiths Fork,

an eventual tributary to the Green River in Wyoming (M. Fowden, Wyoming Game and Fish Department, pers. commun.). Rainbow, brook, brown, golden, and lake trout and coho salmon were introduced into the northern and eastern portions of the Green River drainage before 1934 (Simon 1935). Culture and distribution of nonnative salmonids began in Colorado in 1872 (Wiltzius 1985). Trappers Lake, historically the major source of Colorado River cutthroat trout for stocking throughout Colorado, was planted with Yellowstone cutthroat trout from 1943 to 1950 (Snyder and Tanner 1960).

Nonnative salmonids affect populations of Colorado River cutthroat trout in different ways. Brook trout usually oust most subspecies of inland cutthroat trout when in sympatry, especially at lower elevations and in low-gradient streams (Fausch 1989; M. Fowden, Wyoming Game and Fish Department, pers. obs.). In one portion of Douglas Creek, Wyoming, brook trout effectively replaced Colorado River cutthroat trout between 1982 and 1986 (Oberholtzer 1990). Apparently following a single 1950 planting in a headwater lake, brook trout replaced Colorado River cutthroat trout in the lake and in tributaries throughout the Battle Creek, Wyoming, drainage (Eiserman 1958). Brook trout also supplanted Colorado River cutthroat trout in the headwater tributary of the Colorado River between 1970 and 1975 (Behnke and Zarn 1976). Competition is often suspected as the mechanism leading to replacement, but this has not been demonstrated (Fausch 1988; Griffith 1988). Nevertheless, water temperature can affect the outcome of competitive interactions between these species (DeStaso and Rahel 1994), and this may confer a competitive advantage to brook trout at lower elevations.

Rainbow trout and nonnative subspecies of cutthroat trout readily hybridize with Colorado River cutthroat trout and produce fertile offspring. By 1959, nearly one-third of the spawning run in Trappers Lake consisted of Yellowstone cutthroat trout and occasionally rainbow trout (Snyder and Tanner 1960), which led to the development of a hybrid swarm (Martinez 1988). Also, two previously pure populations in Colorado River tributaries appeared contaminated by rainbow trout genes (Martinez 1988). At least initially, more populations of Colorado River cutthroat trout may have been lost through hybridization than through any other cause (Behnke and Zarn 1976).

A wide variety of land management practices have been suggested to affect populations of Colorado

River cutthroat trout. Binns (1977) considered many foothill streams in Wyoming that contained this subspecies to be degraded by overgrazing. Elevated concentrations of lead (Quinlan 1980) and copper (Jespersen 1981) have been found in the North Fork Little Snake River drainage and may be limiting fish abundance. Haggerty Creek, Wyoming, contains toxic effluents from an abandoned copper mine that have eliminated nearly all fish downstream (Oberholtzer 1987). Ironically, this contamination has isolated populations of Colorado River cutthroat trout in several tributaries of Haggerty Creek and protected them from invasion by brook trout and rainbow trout. Water diversion has reduced flows throughout much of the North Fork Little Snake River watershed. Jespersen (1981) concluded that the abundance of Colorado River cutthroat trout in the North Fork Little Snake River and a tributary, Green Timber Creek, would increase from 42 to 142% if adequate instream flows were returned to each stream. These diversions also have fragmented streams, restricting movement between formerly connected populations and creating small, isolated populations that may be more liable to go extinct.

Even when the effects of land management are discernable, the consequences for fish may be unknown. For example, a sediment spill in Green Timber Creek in May 1988 was presumed to harm Colorado River cutthroat trout. Whereas mean fish counts increased 73% after the spill, mean fish size declined 25%. The abundance of spawning gravel, and thus juvenile fish, seems to have increased, but deeper pools occupied by adults may have been filled in by sediment and reduced the abundance of this age class.

Though this subspecies has been regarded as the "canary in the mine" with regard to habitat degradation (Behnke and Benson 1980), it has also persevered in suboptimal habitats. Binns (1977) noted that Colorado River cutthroat trout sometimes persisted in marginal, degraded habitats, often as the only fish species. Behnke and Zarn (1976) also reported that Colorado River cutthroat trout remained in such habitats despite introductions of rainbow trout, and they considered these populations worthy of preservation for this ability.

Unrestricted angling may also pose a threat to populations of this subspecies. Quinlan (1980) reported capturing 50 Colorado River cutthroat trout in 4 to 6 hours, and four individuals caught 48 trout in 4 hours from the West Branch of the North Fork Little Snake River (Eiserman 1958). In one year, anglers apparently removed at least one-third of the

adult Colorado River cutthroat trout from Ted Creek, Wyoming, and this loss appeared to change the age structure in the stream the following year. Remmick (no date) considered increased fisherman access detrimental to populations of this subspecies.

Current Management

The decline in abundance of this subspecies has been acknowledged by several agencies. Colorado River cutthroat trout are classified as a Category 2 species by the USDI Fish and Wildlife Service and a sensitive species by Regions 2 and 4 of the USDA Forest Service, and designated with special status in Colorado, Utah, and Wyoming. Now, management plans for this subspecies are complete for northwestern Colorado and south-central Wyoming and drafted for west-central Colorado and all of Utah.

Management of this subspecies has taken several forms. Surveys of the distribution of this subspecies have been completed in south-central Wyoming (Oberholtzer 1990), west-central Wyoming (Remmick, no date), and northwestern Colorado (Martinez 1988; D. Vos, White River National Forest, pers. commun.), but undiscovered populations probably remain. In Wyoming, many populations are protected by fishing closures or catch-and-release regulations. In some waters containing this subspecies, Colorado has prohibited harvest and only allows the use of artificial flies and lures. In contrast, Utah has chosen not to apply special regulations to streams containing this subspecies to avoid attracting public attention (Utah Division of Wildlife Resources, unpubl. document). Certain streams thought to contain genetically pure Colorado River cutthroat trout have been artificially barricaded to prevent the invasion of nonnative fishes. Other streams have received human-made structures designed to increase habitat quantity and quality, or are undergoing changes in land management to improve stream habitat. Finally, a few populations have been evaluated by electrophoresis (Leary 1990; Leary et al. 1993) or mtDNA analysis (Shiozawa et al. 1993) to determine their genetic integrity, but most population evaluations have been based only on visual assessments of morphology and meristics (Binns 1977).

Research Needs

Our understanding of this subspecies is minimal. Basic biological information, such as age at maturity,

fecundity, life span, proportion of repeat spawners, spawning frequency, age structure, or even density is lacking for most populations. Furthermore, the timing and magnitude of seasonal movements of most populations and the environmental factors controlling population abundance and structure are unknown. Consequently, we must address such simple biological questions and complex long-term and large-scale problems as: (1) How does the life history of the remaining populations vary? How is this variation affected by land and species management? (2) Do populations seasonally shift their habitat use and position in a watershed? Have we fragmented populations by restricting access to portions of watersheds? Can we calculate the risk of extinction of these populations? Alternatively, if we reconnect streams, how fast will these populations expand into the newly available habitat? Does or can this subspecies form metapopulations? (3) What environmental factors affect the abundance of this subspecies, and how do these effects vary seasonally and by fish life stage? and (4) Historically, how have populations responded to natural disturbances and the ensuing vegetative succession, i.e., what successional sere supports the greatest population density, or what combination of seres are necessary to maintain habitats for all life stages?

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Chapter 3

Rio Grande Cutthroat Trout

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Introduction

The Rio Grande cutthroat trout was once widespread in the upper Rio Grande and Canadian River basins of northern New Mexico and south-central Colorado and in the headwaters of the Pecos River, New Mexico (Sublette et al. 1990; Behnke 1992). It may have occurred as far south as Chihuahua, Mexico (Behnke 1992). Currently, it is restricted primarily to headwater tributaries within its native range. Its southernmost distribution is Indian Creek in the Lincoln National Forest and Animas Creek in the Gila National Forest, southern New Mexico. It ranges north to headwater tributaries of the Rio Grande in the Rio Grande and San Juan National Forests in southwestern Colorado. There are few lake and introduced populations (Colorado Division of Wildlife 1992; Stumpff 1992).

Life History Characteristics

Other than general statements for the species and cursory observations (Sublette et al. 1990), virtually no information is available on the life history of Rio Grande cutthroat trout. Fish spawn in streams from March through July, depending on water temperature (Sublette et al. 1990). Egg production by females is size-dependent and ranges from 200 to 4,500. In colder waters growth is slow, and age at maturity may be 4 years.

Habitat Relations

Specific information on the habitat requirements for spawning, rearing, cover, and feeding for the Rio Grande cutthroat trout are not available. Limited habitat evaluation has been conducted using the General Aquatic Wildlife System in the Santa Fe and

Carson National Forests; however, none of this information is available in reports.

Biotic Interactions

The Rio Grande cutthroat trout evolved with minnow and sucker species in middle to upper elevation (2,000–3,000 m mean sea level) montane streams. These species included the Rio Grande chub and longnose dace in streams in the Rio Grande and Pecos and Canadian river drainages (Sublette et al. 1990). In addition, the Rio Grande sucker was in the Rio Grande drainage, the white sucker and creek chub were in the Pecos and Canadian river drainages, and the southern redbelly dace occurred in the Canadian River drainage. Young-of-the-year and juveniles of these species may serve as prey for adult cutthroat trout.

Non-piscine predators undoubtedly include garter snakes, great blue and other herons, and raccoons. Nevertheless, they are probably unimportant sources of mortality relative to angling or interactions with non-native salmonids. No data are available on the effects of natural predation.

The subspecies is an opportunistic feeder and terrestrial insects may constitute much of the diet in summer. Similar to other salmonids, aquatic macroinvertebrates are undoubtedly a major component of the diet (Sublette et al. 1990). Individuals become more piscivorous as they grow (McAfee 1966; Baxter and Simon 1970). Disease and parasite information is unavailable for wild fish.

Reasons for Concern

No precise data are available on the loss of stream kilometers that once served as habitat for the Rio Grande cutthroat trout, but the distribution of this

subspecies may have declined to 5–7% of its historical range (Stumpff 1992). Because most stocks are now isolated in headwater habitats, gene flow among populations is virtually nonexistent. In addition, poor winter habitat, stream intermittency and deteriorating water quality resulting from drought, and the potential effects of the aftermath of wildfire (see Propst et al. 1992) increase the probability of loss of populations of Rio Grande cutthroat trout.

Causes of the Decline

As with many western native fish species, introduction of nonnative fishes and habitat alteration are primarily responsible for its reduction in range and abundance (Stork 1975; Propst 1976; Sublette et al. 1990; Rinne and Minckley 1991; Behnke 1992).

Probably the greatest threat to the Rio Grande cutthroat trout has been the introduction of nonnative salmonids, principally rainbow trout, brook trout, and brown trout (Behnke and Zarn 1976; Sublette et al. 1990; Behnke 1992). Of these, rainbow trout, also a spring spawner, readily hybridizes with cutthroat trout. The other two salmonid species appear to compete with the Rio Grande cutthroat trout for food and space (cf. Rinne et al. 1981). Although extensive effort has focused on the effect of hybridization with rainbow trout, the nature and extent of the effects of competition with and predation by other introduced salmonids are unstudied.

An apparently lesser effect is that of habitat degradation and loss. In the opinion of several authors (Behnke and Zarn 1976; Sublette et al. 1990; Behnke 1992), livestock grazing on National Forest lands is believed to have had a major effect on the habitat of Rio Grande cutthroat trout. Effects include trampling of streambanks and removal of streamside vegetation (Sublette et al. 1990). Both undercut banks and streambank vegetation serve as resting and hiding cover for trout (Boussu 1954; Meehan 1991). Loss of streamside vegetation facilitates elevation of stream temperatures in summer (Brown and Krygier 1970) and development of anchor ice in winter. Nevertheless, neither the effects or extent of grazing on habitat of Rio Grande cutthroat trout have been specifically studied. Timber harvesting may also affect cutthroat trout habitat through loss of streamside vegetation and large woody material, but this too remains undocumented.

Irrigation diversion accompanying the immigration of early settlers into northern New Mexico re-

sulted in the loss of streams that very likely provided historical Rio Grande cutthroat trout habitat (Sublette et al. 1990). Dewatering effects on cutthroat trout populations likewise have not been the topic of research.

Behnke (1992) suggested that the ease of capture by angling of Rio Grande cutthroat trout relative to that of brown trout resulted in brown trout predominating in the Rio Chiquito near Taos, New Mexico. More detailed information on the effects of angling on Rio Grande cutthroat trout is lacking.

Current Management

The Rio Grande cutthroat trout is considered a sensitive species and a management indicator species by the USDA Forest Service (Stefferdud 1988). The American Fisheries Society lists the subspecies as "protected" (Johnson 1987) and of "special concern" (Williams et al. 1989). Stefferud (1988) has provided the most recent review and description of this subspecies' management. In New Mexico it is considered a sport species and is subject to State Game Commission regulations. The Game and Fish Department has the basic mission to "preserve the natural diversity and distribution patterns of the State's native ichthyofauna" (New Mexico Game and Fish Department 1987). The state has the dual objectives of providing fishing for this subspecies and yet not diminishing it to the point of special regulations. The state's program is coordinated with the Forest Service's land and resource management plans (U.S. Forest Service 1986, 1987). The Forests, through best management practices, monitor water quality in cutthroat trout streams to meet state water quality standards. Also, a broodstock program was initiated by the New Mexico Game and Fish Department in 1987. Both the New Mexico Game and Fish Department and the Colorado Division of Wildlife have draft management plans for this cutthroat trout subspecies (Colorado Division of Wildlife 1992; Stumpff 1992).

Another key component of managing this subspecies is restoration of populations into selected streams. During stream surveys, efforts are made to locate natural barriers or sites suitable for construction of artificial barriers. Removing nonnative salmonids and installing barriers to prevent upstream movement of nonnative trout are vital to maintaining and increasing the range and abundance of this native trout.

After completing a survey of 39 streams in northern New Mexico in summer 1976, Propst (1976) made

a plea for additional inventory surveys to locate new populations of Rio Grande cutthroat trout. This survey and subsequent extensive inventories conducted through the joint efforts of the New Mexico Game and Fish Department and the USDA Forest Service in the mid-1970's and 1980's resulted in a data base depicting the current distribution of Rio Grande cutthroat trout in northern New Mexico.

Three different methodologies have been used to define the purity of populations of Rio Grande cutthroat trout: morphometrics and meristics, electrophoresis, and mtDNA analysis. The first method was used most extensively in earlier (1970-1980) taxonomic analyses (Propst and McInnis 1975; Propst 1976; Behnke 1980). More recent reports to the New Mexico Game and Fish Department (Hartman et al., no date; Moore et al., no date; Riddle and Yates 1990; Davis and Yates 1992) have relied on genetic techniques to evaluate the purity of populations. Based on these analyses, 62 populations of pure or relatively pure Rio Grande cutthroat trout are now known from New Mexico (Stumpff 1992). All but seven of these populations occur on National Forests.

Parallel surveys for Rio Grande cutthroat trout were conducted by the Colorado Division of Wildlife from 1982 to 1987 (Colorado Division of Wildlife 1992). Thirty-nine populations have been identified in Colorado waters; only five are lake populations. Thirty-six of the 39 populations are listed as genetic purity "A" based on morphometric analyses (Behnke 1980).

Estimated population densities for selected cutthroat trout populations in 8 streams in New Mexico varied from 334 to 6,087 fish/ha (mean 1,776 fish/ha); biomasses ranged from 4.3 to 101 kg/ha (mean 22 kg/ha). In contrast, biomasses in the streams in Colorado varied from 3 to 150 kg/ha (mean 35.9 kg/ha; Stumpff 1992).

Research Needs

Streams have been extensively surveyed to locate populations of Rio Grande cutthroat trout and to determine their genetic purity. A priority should be to continue these efforts. It is critical to know the size and location of the resource before it can be managed or researched.

The basic life history attributes of the subspecies should also be determined. Spawning, rearing, feeding, and resting (cover) habitat requirements need to be delineated and the relations between the sub-

species and its habitat need to be investigated. Corollary to this work should be the study of land management on these habitats. Finally, research needs to be conducted on how introduced salmonids (principally brown trout and rainbow trout) limit Rio Grande cutthroat trout populations. In addition, interactions of the Rio Grande cutthroat trout with the other members of the fish community should be investigated.

Research should be closely meshed and integrated with management plans in both states. The studies mentioned above will facilitate management activities to restore this rare native trout to its former range and abundance. Furthermore, researchers should be opportunistic and proactive in synchronizing research with the activities of the game and fish departments of both states and the National Forests. Great effort should be made to conduct this research in the concept of "ecosystem management," or the newly adopted "ecology-based multiple use management" in Region 3.

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Chapter 4

Bonneville Cutthroat Trout

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Introduction

"In this little stream, the trout are more abundant than we have yet seen them. One of our *sober* men took, this afternoon, upward of thirty pounds. These fish would probably average fifteen or sixteen inches in length, and weigh three-quarters of a pound; occasionally, however, a much larger one is seen." This passage from the journal of John Townsend, a trader delivering goods to mountain fur trappers (Townsend, in Trotter and Bisson 1988), describes the Bear River in Wyoming and refers to the native Bonneville cutthroat trout. Historically, the Bonneville cutthroat trout occurred throughout the Pleistocene Lake Bonneville basin, which included portions of Idaho, Nevada, Utah, and Wyoming. The desiccation of Lake Bonneville into the smaller Great Salt Lake and the fragmentation of other stream and lake habitats may have led to three slightly differentiated groups of Bonneville cutthroat trout from the Bear River basin (which includes Bear Lake), the Bonneville basin proper, and the Snake Valley (Behnke 1992). Genetic evidence lends at least partial support to this interpretation; fish from the southern portion of the range can be recognized unequivocally, but northern fish from the Bear River basin share some genetic characteristics with Yellowstone cutthroat trout that suggest a relatively recent separation between these subspecies (Shiozawa and Evans 1994). By 1988, human activities had further reduced the range of Bonneville cutthroat trout to 302 km of streams and 28,293 ha of lakes (Duff 1988).

Habitat for the Bonneville cutthroat trout is widely distributed and variable. It ranges from high-elevation (3,500 m mean sea level) streams with coniferous and deciduous riparian trees to low-elevation (1,000 m mean sea level) streams in sage-steppe grasslands containing herbaceous riparian zones. Bonneville cutthroat trout have adapted to a broad spectrum of conditions throughout their range. Winters

are extremely cold with abundant snowfall. Streams are often ice-covered during the winter and may have formations of instream ice that reduce trout habitat. Spring brings runoff from snowpack in the mountains, followed by low flows during July, August, and September. Lethal and sublethal temperatures may be common throughout the range.

Life History Characteristics

Bonneville cutthroat trout typically spawn during the spring and early summer months at higher elevations (Behnke 1980,1992). In Wyoming, fish usually spawn at lower elevations first, then progress upstream to higher elevations as waters warm (Binns 1981). May et al. (1978) reported Bonneville cutthroat trout spawning in Birch Creek, Utah, in May and June. Fish from Bear Lake, Idaho-Utah, spawned from late April to June (Nielson and Lentsch 1988). Resident fish in St. Charles Creek, Idaho, a tributary to Bear Lake, spawned in April and May (Kershner, pers. obs.). In Lake Alice, Wyoming, fish were predicted to spawn from late May until mid-June (Binns 1981). Spawning temperatures may range from 4 to 10°C (May et al. 1978; L. Jacobson, Payette National Forest, unpubl. data). In Birch Creek, male Bonneville cutthroat trout sexually matured at age 2 and females matured at age 3 (May et al. 1978). A reservoir population of mixed stocks of fish, partly derived from Birch Creek, displayed a similar pattern of age at maturity (D. Hepworth, Utah Division of Wildlife Resources, unpubl. data). Fish appeared sexually mature at age 3 in St. Charles Creek (Kershner, pers. obs.). In Bear Lake, adults normally begin maturing at age 5 but may not spawn until age 10 (Nielson and Lentsch 1988). The average age of spawning fish is 6.8 years (range, age 4 to age 11). Repeat spawners make up less than 4% of the total run.

Fecundity is typically 1,800–2,000 eggs per kilogram of body weight (Behnke 1992). In Birch Creek,

a 147-mm female produced 99 eggs, a 158-mm female produced 60 eggs, and a 176-mm female produced 176 eggs (May et al. 1978), whereas three females ranging from 124 to 248 mm averaged 165 eggs in Raymond Creek, Wyoming (Binns 1981). There is little other information on the fecundity of stream-resident Bonneville cutthroat trout. Fecundity of females in Lake Alice averaged 474 eggs/female (Binns 1981) and in Manning Meadow Reservoir, Utah averaged 994 eggs/female (D. Hepworth, Utah Division of Wildlife Resources, unpubl. data). Incubation times of eggs for naturally spawned Bonneville cutthroat trout are not well-known, but are probably similar to Yellowstone cutthroat trout, which average 310 degree-days (the sum of mean daily temperatures above 0°C) for incubation (Gresswell and Varley 1988). For hatchery-incubated eggs from Manning Meadow Reservoir, degree-days to hatching varied from 329 to 345 (D. Hepworth, Utah Division of Wildlife Resources, unpubl. data).

Fry typically emerge in mid- to late summer, depending on spawning times. Once emerged, fry are poor swimmers and typically migrate laterally to stream margins (Moore and Gregory 1988b). Adfluvial Bonneville cutthroat trout spend 1 or 2 years in streams before migrating to the lake (Nielson and Lentsch 1988; L. Jacobson, Payette National Forest, unpubl. data). It is unknown what proportion of 1- to 2-year migrants is within the population. In 1989, many young-of-the-year Bonneville cutthroat trout emigrated from lower St. Charles Creek to Bear Lake (L. Jacobson, Payette National Forest, unpubl. data).

Growth of resident fish is highly dependent on stream productivity. Since existing populations of resident Bonneville cutthroat trout are limited to smaller, headwater drainages, growth rates tend to be much slower than in lacustrine environments. For example, in Birch Creek, age 1 fish were 84 mm, age 2 fish 119 mm, age 3 fish 158 mm, and age 4 fish 197 mm (May et al. 1978). Growth in two Wyoming streams was faster, and age 4 fish averaged 282–320 mm (Binns 1981). These rates are probably typical for Bonneville cutthroat trout in small streams. In contrast, mature Bonneville cutthroat trout in Bear Lake grow to an average size of 560 mm and 2 kg (Nielson and Lentsch 1988). Age 2 individuals constitute 50% of the fish in Bear Lake, and older fish make up less than 35% of the population. Stocking of young fish, however, may be influencing age structure and growth; between 160,000 and 1,000,000 age 1 fish from 125 to 200 mm have been introduced annually (Nielson and Lentsch 1988).

Likewise, growth in large rivers was probably faster than in streams. Yarrow (1874) reported fish up to 650 mm and 7 kg from the Timpanogos (Provo) River, Utah, but these may have been adfluvial fish from Utah Lake.

Habitat Relations

Habitat relations for Bonneville cutthroat trout are presumed to be similar to those of other cutthroat trout subspecies and other nonanadromous trout. Specific habitats are apparently used for spawning, juvenile rearing, and adult rearing. In addition, these requirements may vary by season. Binns (1981) calculated habitat values for Bonneville cutthroat trout in Wyoming streams using the Habitat Quality Index, but this is a generic model for many trout species and uses cover, bank stability, water velocity, maximum summer stream temperature, stream width, late summer streamflow, annual streamflow variation, nitrate nitrogen, and substrate to classify trout habitat. Most data specific to Bonneville cutthroat trout are anecdotal or unpublished.

In St. Charles Creek, adfluvial Bonneville cutthroat trout typically spawned in pool tails in the lower one-third of the stream, which was characterized by channel gradients less than 1%, high sinuosity, and sorted substrates with a high percentage of fine sediment. Redds typically contained a high percentage of fine sand (less than 1 mm), as well as gravel or cobble (8–100 mm) (Jacobson and Kershner, unpubl. data). Body size was proportional to the size of gravel excavated in the stream.

Resident Bonneville cutthroat trout spawned in higher gradient reaches of St. Charles Creek. Similar patterns have been observed in Salt and Coal creeks, Wyoming (N.A. Binns, Wyoming Game and Fish Department, pers. commun.). Characteristics of these reaches included gradients of 1.5 to 3.5%, low sinuosity, and sequences of steps and pools. Resident spawners were opportunistic, using small pockets of gravel in pools and riffles. These spawning areas generally contained large sand and small gravel (1–16 mm).

Habitat requirements for young Bonneville cutthroat trout are poorly reported in the literature. Other authors, however, have described the location and habitat of cutthroat trout fry (Moore and Gregory 1988a,b; Bozek and Rahel 1991). Moore and Gregory (1988b) reported that coastal cutthroat trout fry used lateral stream habitats associated with com-

plex cover. When they artificially increased cover complexity (Moore and Gregory 1988a) the numbers of fry increased. Bozek and Rahel (1991) found somewhat different results for young-of-the-year Colorado River cutthroat trout. In steep headwater streams, cutthroat trout fry used small backwater pools and upstream dam pools where velocities were low. In lower-gradient streams, fry were also found in backwaters and dam pools, as well as low-velocity areas of lateral scour pools. The authors also found fry in larger habitat units where slow water was interspersed with fast water. A key to habitat use was the proximity of these habitats to redds.

In St. Charles Creek, juvenile cutthroat trout used different channel units depending on the characteristics at the reach scale (L. Jacobson, Payette National Forest, unpubl. data). In all reaches the majority of age 0 and age 1 trout were primarily found in complex pool habitats in summer, fall, and winter. Age 1 trout used habitats associated with wood, e.g., rootwads and woody debris. Run habitat was heavily used in the low-gradient reach by age 1 cutthroat trout in summer.

Adult habitat may limit populations of resident trout in most streams (Behnke 1992). Fluvial habitat for adult Bonneville cutthroat trout is primarily related to the amount and type of cover available and the depth of water. Cover for adult Bonneville cutthroat trout is primarily in deeper pools associated with undercut banks and vegetative cover. It is likely that beaver ponds play an important role as both summer and winter holding habitat for adults (Binns 1981; Remmick et al. 1993). In St. Charles Creek, pools and runs were important habitat features for adult Bonneville cutthroat trout during all seasons and in all stream reaches (L. Jacobson, Payette National Forest, unpubl. data). Riffles were important habitats for adults during summer in low-gradient reaches and during winter in high-gradient reaches.

Most studies on the habitat relations of lacustrine Bonneville cutthroat trout have been conducted in Bear Lake. There, Bonneville cutthroat trout typically inhabit the littoral and pelagic zones during most of the year (Nielson and Lentsch 1988). During the winter, fish were located from 2 to 25 m deep (Wurtsbaugh and Hawkins 1990). In June, trout were found in the littoral zone and at the metalimnetic intercept with the bottom. In August and October trout less than 250 mm were concentrated at the metalimnetic intercept with the bottom (10–20 m) whereas larger fish were evenly distributed in the metalimnion and

profundal zone (15–35 m). Temperature appears to be the major influence on the distribution of Bonneville cutthroat trout in Bear Lake.

Biotic Interactions

In many parts of their range, Bonneville cutthroat trout evolved with june sucker, Utah sucker, mountain sucker, leatherside chub, Utah chub, reddsider, least chub, longnose dace, speckled dace, Bonneville mottled sculpin, and mountain whitefish (Sigler and Miller 1963). In Bear Lake, Bonneville cutthroat trout evolved with Bear Lake whitefish, Bonneville whitefish, Bear Lake cisco (all restricted to Bear Lake), and Bear Lake sculpin.

Interactions between Bonneville cutthroat trout and these fish vary. Suckers, sculpins, and minnows probably provide forage after Bonneville cutthroat trout attain sufficient size to switch from invertebrates to larger prey. Occasionally, sculpins prey on Bonneville cutthroat trout eggs and fry (Sigler and Miller 1963), but sculpins appear to be a minor predator. Many of these fishes feed on insects during part or all of their life history. Since Bonneville cutthroat trout are insectivorous, especially in streams (May et al. 1978), there may be competition for food. It is likely that as the range of Bonneville cutthroat trout has shrunk to the smaller, headwater tributaries, this phase of competition lasts longer in their life history. This is particularly true where Bonneville cutthroat trout co-exist with mountain whitefish.

There has been almost no information published on non-piscine predators. Anecdotal accounts from St. Charles Creek indicate that birds prey on young Bonneville cutthroat trout when they are migrating to the lake (L. Jacobson, Payette National Forest, pers. commun.).

Both terrestrial and aquatic invertebrates appear to be important food items for stream-dwelling Bonneville cutthroat trout (May et al. 1978; Binns 1981). Their diet was diverse during summer in Birch Creek, but consisted primarily of terrestrial insects in late summer and early fall in Trout Creek, Utah (May et al. 1978). Dipterans and debris were the dominant food items for immature trout and terrestrial insects were the dominant prey for mature individuals.

In Bear Lake, the diets of Bonneville cutthroat trout shift as they grow. Trout less than 250 mm primarily ate aquatic and terrestrial insects (Wurtsbaugh and Hawkins 1990). Of the aquatic insects, over 90% were chironomid pupae. As summer progressed, terres-

trial insects became the dominant food item. Ninety-two percent of the diet during August was ants. For intermediate-sized fish (250–350 mm), diets consisted mostly of Bear Lake sculpin during the winter and spring, and fish, aquatic chironomids, and terrestrial insects during summer and fall. Ants and homopterans were the most frequent terrestrial insects in the diet, and chironomid pupae were the most frequent aquatic prey. At 225 mm, fish became piscivorous, and until the fish reached 300 mm they primarily preyed on Bear Lake sculpin. After Bonneville cutthroat trout exceeded 300 mm they switched to other fish prey items. Trout longer than 350 mm relied almost exclusively on a fish diet and preferred Bear Lake cisco during the winter.

A variety of diseases and parasites are found in waters containing Bonneville cutthroat trout. Infectious pancreatic necrosis and infectious hematopoietic necrosis have historically been found in waters throughout Utah but have not been recently observed (R. Goede, Utah Division of Wildlife Resource, pers. commun.). Recently, whirling disease was introduced into the Little Bear River, Utah. Though this disease is currently localized, there is a possibility that it may spread throughout the Bear River system. The parasites *pleistophora* and *epitheliocystis* have been found in the Bear River system and may affect Bonneville cutthroat trout. The bacterial diseases furunculosis and bacterial kidney disease are also found within the system. There is no literature that directly assesses the effect of diseases on Bonneville cutthroat trout.

Reasons for Concern

Prior to European settlement of the Great Basin, Bonneville cutthroat trout were well distributed throughout the historical Bonneville Basin (Behnke 1992) but by the early 1950's it was believed that the Bonneville cutthroat trout was extinct (Cope 1955). Though it is unknown how many lakes contained Bonneville cutthroat trout prior to nonnative fish stocking, fewer than 5% of the thousands of kilometers of stream habitats once occupied by Bonneville cutthroat trout are currently known to be inhabited. Large river systems like the Bear River and Sevier River probably had connected networks of streams enabling Bonneville cutthroat trout to move freely from headwater streams to mainstem rivers. Bonneville cutthroat trout may have used these sections differently during their life history. For example, fish probably spawned and reared in the smaller

tributary streams, then migrated to the larger streams. Given the historical documentation of larger fish in the mainstem Bear and Provo rivers it appears this pattern was likely (Suckley 1874). Today, this access to mainstem rivers is largely nonexistent owing to physical barriers from irrigation, power, and agricultural diversions. Except for the Smiths Fork and Thomas Fork Bear River enclave of Bonneville cutthroat trout, there is little connectivity left within their former range. Furthermore, many fragmented stream habitats within the former range have declined in quality (Binns 1981; Duff 1988; Behnke 1992; Fallau 1992; Remmick et al. 1993; Scully 1993). Recovery strategies have often proposed erecting barriers within a drainage, further isolating Bonneville cutthroat trout populations. Though this may have negative connotations for connectivity, managers have often used these barriers to inhibit hybridization and reduce competition with nonnative salmonids.

Causes of the Decline

Nonnative species have been widely introduced throughout the former range of Bonneville cutthroat trout. These introductions began in the late nineteenth century and have continued (Behnke 1992). Probably the most significant introduction has been the planting of other salmonids. Rainbow trout have been widely introduced throughout the West and pose many problems to native cutthroat trout (Duff 1988). Foremost among these problems is hybridization between the two species; this may cause the loss of coadapted gene complexes within certain Bonneville cutthroat trout populations that enabled these fish to survive catastrophic events such as prolonged drought and associated high water temperatures. In addition, the characteristic phenotype of pure Bonneville cutthroat trout is no longer expressed. Similarly, Bonneville cutthroat trout suffer from hybridization with other subspecies of cutthroat trout. The Yellowstone cutthroat trout has been cultured successfully and is frequently stocked throughout the West (Behnke 1992), including many waters that historically contained Bonneville cutthroat trout.

Competition with nonnative salmonids is also believed to have resulted in the decline of cutthroat trout throughout the western United States (Behnke 1992). In Wyoming, Bonneville cutthroat trout have decreased in four streams (Raymond Creek, Smiths Fork River, Hobbie Creek, and Coal Creek) containing brook trout, brown trout, or both (Remmick et

al. 1993). These species are thought to replace the native fish through competition or predation, but these explanations have not been confirmed (Fausch 1988,1989; Griffith 1988).

Moyle and Vondracek (1985) speculated that introduced brown and rainbow trout may compete with the endemic Lahontan cutthroat in Martis Creek, California. They believed that once other species were introduced it was unlikely that cutthroat trout would regain the original space. In Bear Lake, rainbow trout and lake trout were introduced during the early twentieth century. Nielson and Lentsch (1988) speculated that a gradual decline in Bonneville cutthroat trout in the lake was due to competitive effects.

The abundance and quality of the stream and lake habitat once available to Bonneville cutthroat trout have declined (Binns 1981; Duff 1988; Behnke 1992). The primary causes of habitat loss have been water diversion, degradation of riparian habitats from grazing, road building, mining, and timber harvest. Probably the greatest single cause of habitat loss has been the diversion of streamflows. Diversions have fragmented stream habitats and disconnected tributary streams from mainstem rivers. These diversions reduce streamflow, preventing migration and creating thermal barriers. Many unscreened diversions attract migrating fish into the diversion canals and these fish are lost during irrigation. In St. Charles Creek, diversion during incubation caused a dewatering of 80% of the Bonneville cutthroat trout redds in the stream (Kershner, pers. obs.). I estimated that diversion flows reduced the survival of over 90% of the young Bonneville cutthroat trout in the 1989 year class.

Grazing has been shown to negatively influence stream habitats and stream communities (Keller and Burnham 1982; Platts and Nelson 1985). Poor grazing practices cause stream bank degradation by eliminating or reducing riparian vegetation, physically damaging streambanks, and promoting active erosion. Final results are often a loss of pool habitat, reduced cover, increased water temperature, and substrates that are poorly suited for spawning and food production (Duff 1988; Platts 1991). In Preuss, Dry, and Giraffe creeks, Idaho, habitat features in grazed sections were compared with those in ungrazed sections. Bank stability, the percentage of undercut banks, the width:depth ratio, and the percentage of fine sediment indicated poor habitat quality compared with the ranges of values found in ungrazed streams; trout populations in grazed streams declined from 1980 to 1992 (Fallau 1992). Biologists on the

Bridger-Teton National Forest have surveyed grazed streams in the Thomas Fork Bear River drainage and found that streambank stability was below the desired condition set in forest planning documents (Nelson 1993). Dufour (1992) concluded that grazing along Sugar Pine Creek, Utah, contributed to poor habitat quality. Streams in this area are believed to contain Bonneville cutthroat trout.

Road building may affect Bonneville cutthroat trout populations in two ways. First, during construction sediment is generated that may reach streams during runoff. Native surface roads are particularly susceptible to short-term and long-term erosion from road surfaces and drainage ditches. During surveys of Preuss, Dry, and Giraffe creeks I observed numerous road crossings where fine sediment entered the streams. The second influence is the blockage of Bonneville cutthroat trout migration in streams by poorly designed and placed culverts. In streams throughout Idaho, Utah, and Wyoming I have found numerous culverts that would hinder upstream passage of trout. By preventing upstream migration, culverts effectively isolate small populations. This may have a significant effect on the genetic health of these populations.

Logging has been reported to significantly affect salmonids. Though logging practices probably influenced the quality of habitat in the historical range, there is little evidence of logging effects in the current range. Historical effects included railroad tie driving in the headwater streams of the Bear River. I have observed channels that are still affected by this practice and this may serve as a constraint to some populations of Bonneville cutthroat trout.

Historically, mining severely affected streams in the West (Nelson et al. 1991). Currently, there are few reported mining effects on the remaining populations of Bonneville cutthroat trout, with the possible exception of Hendry's Creek, Nevada (Haskins 1993).

Angling has been shown to depress populations of cutthroat trout (Behnke 1992). Cutthroat trout may be more susceptible to angling pressure than are other salmonids, which could cause a decline in populations that are heavily fished. There are few studies that report the angling effects on Bonneville cutthroat trout. Binns (1981) reported that Bonneville cutthroat trout were "fairly easy to catch," but variation in catchability was noted. In Bear Lake, vulnerability to harvest was highest during the winter (Nielson and Lentsch 1988), probably because of increased angler access.

Current Management

Currently the Bonneville cutthroat trout is listed as a Category 2 species, though recently it has been both petitioned for listing as threatened and proposed for de-listing (D. Hepworth, Utah Division of Wildlife Resources, pers. commun.). The USDA Forest Service, Region 4, has placed the Bonneville cutthroat trout on the sensitive species list and has categorized it as a species of special concern. Similarly, the Bonneville cutthroat trout is listed as a game fish and a sensitive fish species by the Nevada Board of Wildlife Commissioners, as a sensitive species in Wyoming, and as a species of special concern in Utah.

Several existing conservation plans are being used to guide the management of Bonneville cutthroat trout. Idaho is developing special management guidelines for Bonneville cutthroat trout and has signed a statewide conservation agreement with the Forest Service that will address future management of Bonneville cutthroat trout. Nevada has developed a species conservation plan that guides the protection and enhancement of Bonneville cutthroat trout. Utah has recently developed a draft plan that reviews the status of all native cutthroat trout within the state and proposes recommendations for their management, and is developing a conservation agreement with the U.S. Fish and Wildlife Service. Wyoming has a draft 5-year plan that reviews the status of habitats and populations and highlights needed management and research. Many National Forests have developed special standards and guidelines for managing Bonneville cutthroat trout habitat.

State agencies have restricted angling to protect Bonneville cutthroat trout. Idaho and Utah have closed tributaries of Bear Lake to angling during spawning, and Idaho and Wyoming have imposed regulations to reduce harvest in tributaries of the Bear River containing Bonneville cutthroat trout. Also, Bonneville cutthroat trout have been introduced into the Snake Valley of Nevada by the Nevada Division of Wildlife (Haskins 1993). This subspecies has been introduced into Strawberry Reservoir and other waters by the Utah Division of Wildlife Resources (Nielson and Lentsch 1988), and habitats have been protected and enhanced in many waters throughout its range (D. Hepworth, Utah Division of Wildlife Resources, pers. commun.). Also, the genetic purity of many populations has been assessed (Loudenslager and Gall 1980; Leary et al. 1987; Shiozawa et al. 1993; Shiozawa and Evans 1994).

Research Needs

There is currently very little life history information on stream-resident Bonneville cutthroat trout. The most comprehensive studies (May et al. 1978; Binns 1981) examined some life history information, but spawning, fry rearing, and adult rearing requirements have been neglected. There is better information on lacustrine forms, but their juvenile phase in streams is poorly understood.

Habitat relations are also largely speculative, especially in streams. The best information on habitat relations comes from Binns (1981, 1986) and Jacobson (unpubl. data), and though the latter documentation details habitat relations for all life stages by season, it represents a sample of one stream. Given the distribution of the current populations, more information on habitat requirements is needed.

The decline of native cutthroat trout after introductions of nonnative fishes has been well documented, but there is no conclusive explanation for this decline, e.g., competition has been hypothesized but never demonstrated. Studies that examine competition and other interactions between nonnative salmonids and Bonneville cutthroat trout should be initiated.

The knowledge of the distribution of this subspecies is spotty. We need a full assessment of the historical and current range to accurately document the decline of Bonneville cutthroat trout. In addition, we need to establish the population trends. And given the existing small populations and fragmented habitats, we need to learn how to design effective reserves for Bonneville cutthroat trout.

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Chapter 5

Yellowstone Cutthroat Trout

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Introduction

The Yellowstone cutthroat trout is more abundant and inhabits a greater geographical range than does any other nonanadromous subspecies of cutthroat trout (Varley and Gresswell 1988). The Yellowstone cutthroat trout was indigenous to the Snake River upstream from Shoshone Falls, Idaho, and the Yellowstone River above the Tongue River, Montana (Behnke 1992). Although there are some disagreements concerning the evolutionary history of cutthroat trout and various cutthroat trout subspecies (Behnke 1992; Stearley 1992; Stearley and Smith 1993), the most recent incursion of Yellowstone cutthroat trout into the Yellowstone River drainage is apparently related to the retreat of glacial ice approximately 12,000 years ago (Richmond and Pierce 1972). Individual populations of the Yellowstone subspecies have evolved numerous life history characteristics in response to the diverse environments in which they have been isolated since the last glacial retreat; human activities, however, have resulted in a substantial reduction in the historical distribution of this subspecies.

Life History Characteristics

Spawning patterns.—Yellowstone cutthroat trout spawn exclusively in running water, and there are three spawning patterns:

(1) Resident populations generally spawn within their home range in lotic systems. Fish may migrate, but spawners do not enter tributary streams. Kelly (1993) recorded movement of mature Yellowstone cutthroat trout in the Yellowstone River between Yellowstone Lake and the Upper Falls of the river (28 km). Approximately 52% of recaptured fish were collected in the segment where they were initially

marked; 41% moved upstream, and 7% moved downstream. After emergence, fry may move either upstream or downstream or remain near the redd (Varley and Gresswell 1988).

(2) Fluvial populations migrate from streams and rivers into tributaries to spawn. This pattern has been documented in the Yellowstone River in Montana (Clancy 1988), several drainages in the Snake River in Idaho (Thurrow et al. 1988), and in the Yellowstone River (below the Lower Falls) and Lamar River in Yellowstone National Park (Varley and Gresswell 1988). Juveniles may emigrate as fry or spend 1 to 3 years in natal tributaries before returning to the mainstem (Thurrow et al. 1988; Varley and Gresswell 1988).

(3) Adfluvial populations live in lakes and ascend inlets or descend outlets to spawn. Although juveniles from most tributaries to Yellowstone Lake migrate to the lake shortly after emergence, some may remain in their natal stream for one or more years if the habitat is suitable (Varley and Gresswell 1988). Returns of marked fish suggested long-term (more than 2 years) lotic residency for some Yellowstone cutthroat trout that were spawned in Pelican Creek, a tributary of Yellowstone Lake (Gresswell et al., in press). Outlet spawning is less common, but has been documented in Yellowstone Lake (Ball and Cope 1961), Heart Lake (Varley and Gresswell 1988), and Pocket Lake (U.S. Fish & Wildlife Service, unpubl. data) in Yellowstone National Park. Fry move upstream to the lake after emergence, and this behavior appears to be heritable (Raleigh and Chapman 1971; Bowler 1975).

Homing by Yellowstone cutthroat trout spawners is believed to influence life history diversity through reproductive isolation (Gresswell et al., in press). Ball (1955) documented natal homing (return of adult spawners to the area of their birth) in Arnica Creek, a tributary of Yellowstone Lake. Repeat homing behavior (individual spawners returning to the same

tributary in successive years; McCleave 1967) has been observed for adfluvial spawners from Yellowstone Lake (Cope 1957a; Jones et al. 1984) and fluvial spawners from the Yellowstone River in Montana (Clancy 1988) and the Blackfoot and South Fork Snake rivers in Idaho (Thurrow et al. 1988). In-season homing was experimentally investigated when individual adults returned to a spawning area after dislocation (McCleave 1967; Jahn 1969; LaBar 1971).

Straying during the spawning migration is low. Between 1949 and 1955, 18,836 cutthroat trout from Yellowstone Lake were tagged as they entered Arnica, Chipmunk, Clear, Grouse, and Pelican creeks to spawn (Cope 1957a). Of 244 adults that returned to spawn in subsequent years, 97% were collected in the stream where they were originally tagged. In a separate study, Ball (1955) marked three groups of immature cutthroat trout in 1950 and 1951 as they migrated from Arnica Creek to Yellowstone Lake. Between 16 and 25% of these fish eventually returned to spawn in Arnica Creek, but none were recovered in the five other tributaries being monitored during that period. More recently, 23% of 42,229 cutthroat trout marked at Clear Creek in 1979 returned to spawn again, but only 1% of the marked fish were collected in Pelican or Cub creeks (Jones et al. 1985). Only 10 of 333 Yellowstone cutthroat trout tagged in tributaries to the Blackfoot River failed to return to the stream in which they were marked; nine of these fish strayed between two streams that entered the Blackfoot River 400 m apart (Thurrow 1982).

Migration timing.—Substantial differences in migration timing have been documented for tributaries to Yellowstone Lake (Gresswell et al., in press). Physical characteristics of a drainage directly influence the hydrologic cycle in a basin (Morisawa 1968), and a strong relation between timing of spawning migrations of Yellowstone cutthroat trout and hydrographic stage and water temperature has been observed in tributaries to the lake (e.g., Ball and Cope 1961; Jones et al. 1990). Throughout the range of Yellowstone cutthroat trout, spawner abundance generally increases as water temperature rises and discharge decreases from spring runoff peak (Varley and Gresswell 1988; Byorth 1990; Thurrow and King 1994). During the early portion of the spawning migration in Clear Creek, some fish have been observed repeatedly moving into and out of tributaries without spawning (USFWS, unpubl. data).

Yellowstone cutthroat trout generally spawn between March and August, and migrations begin

when temperatures approach 5°C (Varley and Gresswell 1988; Byorth 1990; Thurrow and King 1994). Although Yellowstone cutthroat trout spawners will enter tributaries prior to major increases in discharge, most fish migrate after the spring peak (Ball and Cope 1961; Jones et al. 1990; Thurrow and King 1994). Daily upstream migrations increase to a peak in concordance with water temperature, usually between 1300 and 1700 hours (Byorth 1990; Jones et al. 1990). For 13 years between 1977 and 1992, maximum daily water temperature in Clear Creek, a tributary to Yellowstone Lake, ranged from 10 to 14.2°C on the date of peak spawning migration (USFWS, unpubl. data). In 1991, maximum daily water temperature in Pine Creek, a tributary to the South Fork Snake River, ranged from 16 to 20°C during the Yellowstone cutthroat trout spawning migration (Thurrow and King 1994).

In most tributaries to Yellowstone Lake, Yellowstone cutthroat trout spawners remain in streams from 6 to 25 days (Varley and Gresswell 1988), but in some larger tributaries, adfluvial spawners may not return to the lake for many months (Jones et al. 1982). Males generally migrate into spawning tributaries earlier than do females and remain in spawning areas longer (Ball and Cope 1961). Emigration of postspawners is generally nocturnal while discharge is high during the early portions of the spawning migration, but most fish move during the day as the run progresses (Varley and Gresswell 1988).

Characteristics of spawning fish.—In tributaries to Yellowstone Lake, older and larger Yellowstone cutthroat trout migrate first (Ball and Cope 1961; Jones et al. 1990). Data suggest that older and larger individuals also migrate farther upstream (Cope 1957b; Dean and Varley 1974); this behavior has been noted for other fishes (Briggs 1955). Nevertheless, fish usually spawn earlier at lower elevation sites. Age, length, weight, and condition factors decline as the spawning migration progresses (Jones et al. 1990).

Mean age of spawners varies geographically. Thurrow et al. (1988) reported that most resident fish in the upper Snake River in Idaho matured at age 4 or 5. Most Yellowstone cutthroat trout in Henrys Lake mature at age 3 (Thurrow et al. 1988). Clancy (1988) considered fish age 3 and older as mature in the Yellowstone River between Corwin Springs and Springdale, Montana. Between 1987 and 1992, mean age for spawners at Clear Creek, a tributary to Yellowstone Lake, was 5.8 years (Gresswell et al., in press).

Average size of Yellowstone cutthroat trout spawners is also variable. In Idaho, few fish less than 200 mm were mature, most fluvial spawners exceeded 275 mm, and mean length varied between 300 and 500 mm (Thurrow et al. 1988). In the Yellowstone River in Montana, Clancy (1988) grouped fish over 300 mm as adults, and spawners from two tributaries to the river ranged from 322 to 368 mm in 1988 and 1989 (Byorth 1990). Benson and Bulkley (1963) found that Yellowstone Lake fish above 300 mm were mature, and most fish less than 250 mm were immature. Data collected since 1985 suggest that mean length of Yellowstone cutthroat trout spawners from individual tributaries to Yellowstone Lake ranged from 305 to 405 mm (USFWS, unpubl. data). In small sub-alpine lakes and streams Yellowstone cutthroat trout may mature between 100 and 130 mm.

Angler harvest can affect the mean age and length of Yellowstone cutthroat trout spawners (Gresswell and Varley 1988). At Clear Creek, mean age of Yellowstone cutthroat trout declined to 3.9 years in the mid-1960's when angler success (number of fish captured/hour) and mean length of captured fish were declining. Since restrictive regulations were implemented in the early 1970's, the average age in the spawning run has increased. Age 9 Yellowstone cutthroat trout have been collected annually in Clear Creek since the late 1970s; maximum age of spawners has increased to 11 years old. At LeHardy Rapids (Yellowstone River, approximately 6 km below Yellowstone Lake), annual monitoring demonstrated an increase in mean age from 3.7 years immediately following the implementation of catch-and-release regulations in 1973 to 6.1 years in 1986 and 1989 (Jones et al. 1992). Corresponding increases in length have been observed in both locations.

Thurrow et al. (1988) reported that except for the Henrys Lake Hatchery migration, females were more abundant than were males in fluvial spawning populations sampled in Idaho. Male:female ratios varied from 0.37:1 to 0.17:1 in the Blackfoot River (Thurrow 1982), and Moore and Schill (1984) reported a male:female ratio of 0.83:1 in the South Fork Snake River. Females are also more abundant in adfluvial spawning migrations in tributaries to Yellowstone Lake. Males often dominate the early portion of spawning migrations, but the proportion of males decreases as the spawning migration progresses (USFWS, unpubl. data). Between 1945 and 1953, mean male:female ratios for six tributaries ranged from 0.61:1 to 0.74:1 (Ball and Cope 1961). Estimates

for 13 sample years between 1973 and 1992 at Clear Creek range from 0.52:1 to 0.75:1 (USFWS, unpubl. data).

An anomalous situation exists in the Yellowstone River below Yellowstone Lake. Since 1976, males have been more numerous than females in most annual dip-net samples from LeHardy Rapids. Male:female ratios were 0.73:1 and 0.79:1 in 1974 and 1975, but since 1976, the male:female ratio has dropped below 1.06:1 only three times (1982, 1986, and 1989). The mean male:female ratio between 1976 and 1991 was 1.35:1. Because these estimates are based on weekly surveys, they may not be directly comparable to male:female ratios obtained from fish traps. Yet samples at LeHardy Rapids are collected throughout the spawning migration, sample sizes are large, and methods have remained unchanged since 1974 (Jones et al. 1992). The 1973 change in angling regulations may explain this phenomenon.

The preponderance of males has been observed elsewhere. Byorth (1990) reported that males dominated the early portions of the spawning migration in Cedar Creek, but as the migration peaked the male:female ratio approached 1:1. Berg (1975) reported similar trends in Cedar Creek. Males were also more abundant in another Yellowstone River tributary, Tom Miner Creek, in 1988 and 1989. Male:female ratios in these fluvial spawning migrations may vary from other reported values because of differences in habitat and life history development, but the low number of spawners in the samples may influence results.

Spawning frequency.—Repeat spawning is common for Yellowstone cutthroat trout (Clancy 1988; Thurrow et al. 1988; Varley and Gresswell 1988), but the prevalence of iteroparity can be affected by angler harvest (Varley and Gresswell 1988). Ball and Cope (1961) reported that first-time spawners composed up to 99% of spawning migrations in Yellowstone Lake during a period when angler harvest was greater than the estimated maximum sustained yield (325,000 trout; Benson and Bulkley 1963). But at least 23% of 42,229 Yellowstone cutthroat trout marked at Clear Creek in 1979 spawned again between 1980 and 1984 (Jones et al. 1985). Repeat spawners represented up to 15% of some resident and fluvial migrations in Idaho (Thurrow et al. 1988). Thurrow (1982) found that 93% of repeat spawners were females.

Additional spawning may be in either consecutive or alternate years (Thurrow et al. 1988; Varley and Gresswell 1988). Using putative spawning erosion on scales, Bulkley (1961) concluded that consecutive-

year spawners were more common in tributaries to Yellowstone Lake. At Clear Creek, however, spawners marked in 1979 returned most frequently in alternate years (1980–1984; Jones et al. 1985). Varley and Gresswell (1988) reported that alternate-year spawning was more common in populations at higher elevations. The pattern of repeat spawning is probably related to growth, parasitic infection, and other physiological factors (Ball and Cope 1961). In the Yellowstone River between Corwin Springs and Springdale, Yellowstone cutthroat trout that spawned during consecutive years consistently exhibited the slowest growth (Clancy 1987).

Based on recaptures of tagged fish, Ball and Cope (1961) reported that average instream mortality of Yellowstone cutthroat trout spawners was 48% in 5 tributaries of Yellowstone Lake between 1949 and 1953. Welsh (1952) reported that in 1951 and 1952, 28% of Yellowstone cutthroat trout spawners in Arnica Creek died near spawning sites and another 1% died before postspawning emigration was complete. At Clear Creek, estimates of instream mortality based on total counts of upstream and downstream migrants averaged 13% for 5 sample years (1977–1979, 1983, and 1984; Jones et al. 1985). In recent years, estimates of instream mortality at Clear Creek have increased (mean = 31% for 1987, 1988, 1991, and 1992; USFWS, unpubl. data) although the relative influence of changes in monitoring procedures and increased numbers of white pelicans *Pelecanus erythrorhynchos* has not been investigated.

Fecundity and early development.—Fecundity is related to length, weight, or age of fish (Bagenal 1978), and changes in mean length and age affect population fecundity (total number of eggs deposited by females; Bagenal 1978). Although relative fecundity (number of eggs/kg of female body weight; Bagenal 1978) has remained unchanged (2,633 eggs/kg; Jones et al. 1985), population fecundity at Clear Creek has risen from 6.2 million eggs in the 1950's to an average of almost 32 million eggs between 1975 and 1992 (USFWS, unpubl. data). Average fecundity of female Yellowstone cutthroat trout has risen in association with increases in mean length, and population fecundity remains high despite a decline in spawner abundance observed at Clear Creek in recent years (USFWS, unpubl. data).

Fecundity of Yellowstone cutthroat trout from Henrys Lake, Idaho, averaged 1,577 and 2,930 eggs/female (mean lengths of 319 mm and 518 mm; Thurow et al. 1988). Moore and Schill (1984) reported

a mean fecundity of 1,413 eggs for females collected from the South Fork Snake River (mean length = 377 mm). At Clear Creek (Yellowstone Lake), the estimated mean fecundity for Yellowstone cutthroat trout in 1992 was 1,393 eggs/female (mean length = 394 mm; USFWS, unpubl. data).

Egg mortality of Yellowstone cutthroat trout in natural redds was estimated to range between 12 and 42% in 3 tributaries to Yellowstone Lake (Mills 1966); mortality was associated with inadequate water flow through gravel. Ball and Cope (1961) estimated 60–70% egg mortality. Angler wading may reduce survival; 83% of Yellowstone cutthroat trout eggs and pre-emergent fry were killed by twice-daily wading (Roberts and White 1992).

Eggs generally hatch in 25–49 days (310 Celsius temperature units, sum of mean daily temperatures above 0°C), and juveniles emerge from the gravel 2 weeks later (Ball and Cope 1961; Mills 1966; Kelly 1993). Juveniles often move to shallow, slow-flowing areas, and migratory individuals soon begin to emigrate (Varley and Gresswell 1988). Although young-of-the-year Yellowstone cutthroat trout are locally numerous in the Yellowstone River below Yellowstone Lake, fish less than 250 mm are not common (Schill and Griffith 1984; Kelly 1993). Kelly (1993) reported that numbers of young-of-the-year fish declined over 90% within 25 days after peak emergence in 1990 and 1991. Few juveniles were observed, and most were found in the segment between Sulfur Caldron and the Upper Falls.

Thurow et al. (1988) reported that in many drainages in Idaho, fry migrate downstream shortly following emergence, whereas juvenile Yellowstone cutthroat trout do not emigrate from some tributaries for 1 to 3 years. Both patterns have been observed in tributaries to Yellowstone Lake (Benson 1960; Gresswell et al., in press) and in the Yellowstone River drainage in Montana (Byorth 1990). Welsh (1952) suggested that the distance from redd to stream mouth directly influenced the length of time that fry remained in tributaries to Yellowstone Lake; those in the upper reaches of Arnica Creek often remained in the stream over winter. Thurow et al. (1988) reported a density-dependent downstream migration related to the abundance of suitable habitat.

Growth.—Growth of Yellowstone cutthroat trout is variable and dependent on population and environmental conditions. Growth rate generally increases as elevation decreases. Thurow et al. (1988) reported that migratory stocks grow faster than do

nonmigratory stocks because of the greater growth potential in higher-order mainstem reaches. Thurow et al. (1988) reported that growth of individuals in migratory populations is greatest following emigration from natal areas and prior to maturity.

Males generally grow faster than do females in Henrys Lake (Irving 1955) and Yellowstone Lake (Bulkley 1961; USFWS, unpubl. data). The largest individuals sampled in Yellowstone Lake were males, but Varley and Gresswell (1988) suggested that this may be due to greater longevity rather than to faster growth. Recent information from Yellowstone Lake and Clear Creek indicates that many large (over 450 mm) individuals are immature (USFWS, unpubl. data). In an environment where the annual growing season is short, somatic growth may be encouraged by postponement of maturity and the associated demands of gonadal development.

In the Blackfoot River and Willow Creek drainages, Idaho, Yellowstone cutthroat trout reach 8 or 9 years of age, lengths greater than 600 mm, and weights from 2 to 4 kg (Thurow et al. 1988). Maximum size in Yellowstone Lake is somewhat lower (over 500 mm and 1.5 kg), but Yellowstone cutthroat trout in Heart Lake, Yellowstone National Park, can exceed 5 kg. Eight species of fish evolved in Heart Lake, and Yellowstone cutthroat trout are believed to be highly piscivorous in this lacustrine environment.

Varley and Gresswell (1988) summarized "typical" back-calculated lengths for Yellowstone cutthroat trout from Carlander (1969): age 1, 100 mm; age 2, 180 mm; age 3, 240 mm; age 4, 310 mm; age 5, 370 mm; age 6, 410 mm. Similar values for growth of Yellowstone cutthroat trout from Yellowstone Lake for 20 years between 1969 and 1992 were obtained: age 1, 60 mm; age 2, 140 mm; age 3, 240 mm; age 4, 310 mm; age 5, 350 mm; age 6, 390 mm; age 7, 420 mm; age 8, 450 mm; age 9, 470 mm (USFWS, unpubl. data). Many other data are available (Irving 1955; Laakso 1956; Laakso and Cope 1956; Bulkley 1961; Benson and Bulkley 1963; Irving 1979; Thurow 1982; Moore and Schill 1984; Corsi 1988; Shepard 1992; USFWS, unpubl. data).

Age analysis for Yellowstone cutthroat trout has primarily relied on the use of fish scales. Scales form when fish are approximately 41 to 44 mm in Yellowstone Lake (Brown and Bailey 1952; Laakso and Cope 1956). Laakso and Cope (1956) validated the use of scales up to age 2. The authors found that some fish did not form an annulus until the end of the second year of growth, and criteria to distinguish

"normal" and "retarded" scale formation in the Yellowstone Lake watershed were established. Laakso (1955) maintained that criteria for establishing age at first annulus (on scales) in the Yellowstone Lake drainage have general applicability, but the universality of this hypothesis has not been determined.

The frequency of normal scales appears to be related to growth rate (Laakso 1955). In a review of populations throughout the range of the Yellowstone cutthroat trout, Lentsch and Griffith (1987) reported that the lack of a first-year annulus was related to temperature within the natal stream. They suggested that when accumulated Celsius temperature units were 720 or fewer, all fish lacked an annulus at the end of the first season of growth. All fish formed an annulus if the Celsius temperature units were 1,500 or greater.

Habitat Relations

Yellowstone cutthroat trout occupy diverse habitats. Lacustrine populations inhabit waters from the size of small beaver ponds to large lakes (e.g., Yellowstone Lake, 35,400 hectares). Varley and Gresswell (1988) reported that populations were historically common in large rivers such as the Snake River above Shoshone Falls, Idaho (mean annual flow, 156 m³/s), and the Yellowstone River near Miles City, Montana (mean annual flow, 321 m³/s). In contrast, Yellowstone cutthroat trout can be found in first-order tributaries with mean widths of 1 m and discharge as low as 0.06 m³/s.

Yellowstone cutthroat trout are well adapted to cold, harsh environments. Data reviewed by Carlander (1969) suggested optimum water temperatures between 4.5 and 15.5°C for the subspecies. Dwyer and Kramer (1975) reported the maximum "scope for activity" at 15°C (difference between maximum and minimum metabolic rates) for a sample of cultured cutthroat trout (age 1+). Yellowstone cutthroat trout collected from Yellowstone Lake under 1 m of ice were actively feeding in water 0 to 4°C (Jones et al. 1979). Populations exist in streams in Yellowstone National Park with summer maxima between 5 and 8°C (Jones et al. 1979). Isolated populations in alpine and subalpine areas overwinter for up to 8 months in small streams with low temperatures and extreme ice conditions (Varley and Gresswell 1988).

Although Yellowstone cutthroat trout are currently associated with cold water habitats, Varley and

Gresswell (1988) reported that water temperatures within portions of the historical range exceeded 26°C. Most of these large-river, warm-water populations have been extirpated, yet several populations have been documented in geothermally heated streams in Yellowstone National Park with an ambient water temperature of 27°C (Varley and Gresswell 1988). Yellowstone cutthroat trout apparently survive under these extreme conditions by locating thermal refugia. Kelly (1993) suggested that cutthroat trout were excluded from Alum Creek, a tributary to the Yellowstone River in Yellowstone National Park, because summer water temperatures often exceeded 22°C.

Yellowstone cutthroat trout tolerate a broad range of chemical conditions. Varley and Gresswell (1988) reported that the subspecies has been collected from waters in Yellowstone National Park with total dissolved solids ranging from about 10 to 700 mg/L. They speculated that conditions were more variable in the historical range (e.g., waters in the Bighorn River drainage, Wyoming, have total dissolved solids exceeding 2,000 mg/L; U.S. Geological Survey, unpubl. data). Alkalinity is relatively low (mean = 64 mg CaCO₃/L) in most areas of Yellowstone National Park, but waters in the upper Snake River basin exceed 150 mg CaCO₃/L (Thurow et al. 1988). Mean alkalinity for three tributaries used by fluvial spawners from the Yellowstone River in Montana ranged from 46 to 378 mg CaCO₃/L (Byorth 1990). Although populations of Yellowstone cutthroat trout have been documented in waters with pH from about 5.6 to over 10.0, none have been observed where pH is below 5.0 (Varley and Gresswell 1988). Kelly (1993) reported that unsuitable water quality precluded survival of Yellowstone cutthroat trout in three tributaries to the Yellowstone River in Hayden Valley, Yellowstone National Park; these streams are characterized by widely fluctuating pH resulting from poor buffering capacity.

Spawning streams are most commonly perennial with groundwater and snow-fed water sources; gradient is usually below 3% (Varley and Gresswell 1988). Varley and Gresswell (1988) reported that the use of intermittent streams for spawning is not widely documented, but spawning has been observed in intermittent tributaries to Yellowstone Lake. In these streams fish spawn during spring runoff, and fry emigrate in July and August, prior to stream desiccation. Although many fry and some adults may become stranded as discharge drops, Varley and

Gresswell (1988) suggested that spawning in intermittent streams may provide a reproductive advantage over nonindigenous fall-spawning salmonids that have been introduced throughout the range of the Yellowstone cutthroat trout.

Varley and Gresswell (1988) suggested that Yellowstone cutthroat trout spawn wherever optimum temperature and substrate are found, but this may be an oversimplification. Cope (1957b) reported that forest cover had little effect on the distribution of redds in tributaries to Yellowstone Lake, and spawners did not always congregate in areas with the greatest concentration of spawning gravel. Thurow and King (1994) noted that in Pine Creek, Yellowstone cutthroat trout spawners selected different sites for spawning in 1991 and 1992; severe drought in 1992 would have caused dewatering at sites used the previous year. The authors emphasized the importance of other physical cues, such as water velocity, for locating redds in areas with a high probability of hatching success and fry survival. Water depth is correlated with water velocity, and this variable may also provide an important physical cue.

Varley and Gresswell (1988) reported that optimum size for gravel in Yellowstone cutthroat trout spawning areas is 12–85 mm in diameter. In 11 redds from Cedar Creek, Byorth (1990) estimated approximately 74% (by weight) gravel (2–63.5 mm in diameter) and 17% cobble (63.5–256 mm in diameter). Yellowstone cutthroat trout in Pine Creek spawned in areas where substrate was less than 100 mm in diameter (Thurow and King 1994). Approximately 60% of the substrate was in the 16- to 64-mm size-class, 15% was in the 6.4- to 16-mm size-class, and 20% was less than 6.4 mm in diameter. Thurow and King (1994) found no significant change in composition of undisturbed substrate near redds from the start to the end of incubation.

Mean size of 66 redds measured by Thurow and King (1994) was 1.58 m long by 0.60 m wide; redds encompassed an area of approximately 1 m². Yellowstone cutthroat trout spawned in water 9 to 55 cm deep in Pine Creek, but over 80% of the redds were at depths between 10 and 30 cm deep (Thurow and King 1994). Average depth of redds in Pine Creek was 20 cm beside the pit and 21 cm upstream from the pit. In a smaller tributary (Cedar Creek), Byorth (1990) reported that 86% and 75% of Yellowstone cutthroat trout redds were constructed at depths of 9.1 to 15.2 cm in 1988 and 1989. Mean depth of redds in Cedar Creek was approximately 12 cm in both years.

Water velocities within 5 cm of completed redds were 16 to 73 cm/s in Pine Creek, and the average was 42 cm/s beside the redd and 46 cm/sec upstream from the redd (Thurrow and King 1994). Mean current velocity at redds in Cedar and Tom Miner creeks averaged approximately 24 cm/s and 38 cm/s (Byorth 1990). Velocities ranged from 0 to 68 cm/s in Cedar Creek, but most redds were found at velocities between 16 and 27 cm/s. Water velocity was 14–71 cm/s near redds in Tom Miner Creek (Byorth 1990).

Thurrow and King (1994) observed superimposition of redds, generally laterally or immediately downstream of existing redds. Byorth (1990) reported superimposition of redds in Cedar and Tom Miner Creeks, and superimposition has been documented in tributaries to Yellowstone Lake (Mills 1966). Thurrow and King (1994) suggested that because most eggs were deposited in the center of the upstream edge of the tailspill, redd superimposition that is located laterally or downstream of the tailspill may not disturb the eggs.

In streams, fry generally seek areas of low velocity (Varley and Gresswell 1988). Yellowstone cutthroat trout fry in Cedar and Tom Miner creeks used similar habitat. Mean depth of locations used by fry in both streams was approximately 11 cm (range 3–24 cm; Byorth 1990). Water velocities were also similar (3 and 5 cm/s for Cedar and Tom Miner creeks), and approximately 50% of fry were located where velocities exceeded 2 cm/s (Byorth 1990). Stream substrate at sites used by Yellowstone cutthroat trout fry differed between the two streams; these differences probably reflected differences in available substrate materials (Byorth 1990).

In late winter (March–April) at water temperatures ranging from 4 to 7°C, Griffith and Smith (1993) found juvenile Yellowstone cutthroat trout concealed in water shallower than 0.5 m within 1 m of the wetted perimeter of the stream. Of seven sites sampled in the South Fork Snake River, 87% of the fish captured were age 0 Yellowstone cutthroat trout, 2% were age 1 Yellowstone cutthroat trout, and 11% were brown trout (Griffith and Smith 1993). Density of age 0 Yellowstone cutthroat trout increased as the substrate size of unembedded cover increased. From 61 to 66% of the juvenile trout in concealment emerged at night (Griffith and Smith 1993).

Adfluvial fry usually begin emigration soon after emergence, but some may overwinter in the natal stream. After emigration from natal streams, fry con-

gregate in shallow water along the shoreline prior to movement into deeper water (Gresswell and Varley 1988). Apparently in Yellowstone Lake most juveniles (through age 2) are pelagic (Gresswell and Varley 1988). Plankton are abundant in these areas, and the vast size of the pelagic area provides protection from predation by larger individuals.

Adfluvial Yellowstone cutthroat trout move into the littoral zone after maturation and apparently remain there throughout the year (Gresswell and Varley 1988). A shift in food preference is associated with the shift in habitat, and the proportion of larger macroinvertebrates in the diet increases (Benson 1961). Mature individuals are especially prominent during spawning migrations as they travel along the shoreline to tributaries. Because most angler use is focused on the shallow, near-shore areas, older and larger Yellowstone cutthroat trout are vulnerable to angler harvest. Scarcity of juvenile Yellowstone cutthroat trout (through age 2) in the angler catch is assumed to be associated with their residence in pelagic areas (Gresswell and Varley 1988).

Biotic Interactions

Except where barriers limited access (e.g., Waha Lake, Idaho, and Crab Creek, Washington), rainbow trout have replaced the Yellowstone cutthroat trout in the Columbia River Basin below Shoshone Falls on the Snake River (Behnke 1992). The falls may have been formed 30,000 to 60,000 years ago during the Bonneville floods (Malde 1965), or as recently as 14,500 years ago (Oviatt et al. 1992). Above the falls, Yellowstone cutthroat trout evolved with 10 other fish species (Thurrow et al. 1988). In Yellowstone National Park, seven of these fishes were historically sympatric with Yellowstone cutthroat trout in the Heart Lake drainage (Jordan 1891; Smith and Kendall 1921; Dean and Varley 1974). On the east side of the Continental Divide only longnose dace were historically sympatric with the Yellowstone cutthroat trout above the Upper Falls of the Yellowstone River (Benson and Bulkley 1963). Below the falls, mountain whitefish, mottled sculpin, longnose sucker, white sucker, and longnose dace were all historically found in the Yellowstone River (Clancy 1988); the white sucker, however, has not been collected in Yellowstone National Park (Varley and Schullery 1983).

There are many predators in the range of the Yellowstone cutthroat trout. Birds may have the greatest effect on populations in the Yellowstone Lake

drainage. The size of fish selected and biomass consumed per day vary among bird species (Davenport 1974; Swenson 1978; Swenson et al. 1986). Estimated total biomass of cutthroat trout consumed by birds near Yellowstone Lake was 117,100 and 83,800 kg for 1973 and 1974 (Davenport 1974).

Although white pelicans were estimated to remove 350,000 Yellowstone cutthroat trout (approximately 105,900 kg) annually in the 1920's (based on population estimates of 500 to 600 pelicans; Ward 1922), Davenport (1974) argued that the estimate of 3.6 kg fish/pelican/day was high. Using an estimate of 1.3 kg fish/pelican/day, she estimated that biomass of Yellowstone cutthroat trout consumed by white pelicans was approximately 16,800 kg (195 pelicans) and 34,500 kg (400 pelicans) in 1973 and 1974 (Davenport 1974).

Grizzly bears (*Ursus arctos horribilis*) and bald eagles (*Haliaeetus leucocephalus*) also commonly feed on Yellowstone cutthroat trout (Mealey 1980; Swenson et al. 1986; Reinhart 1990). Swenson et al. (1986) found that during the breeding season (April-August), Yellowstone cutthroat trout accounted for approximately 23% of the diet of bald eagles in Yellowstone Lake, the Yellowstone River and their tributaries above Upper Falls, and Lewis, Shoshone, and Heart lakes. Eagles consumed Yellowstone cutthroat trout almost exclusively during the peak spawning period in Yellowstone Lake (May-July, Ball and Cope 1961; USFWS, unpubl. data), switching to flightless birds as fish became less available. In the Snake River and its major tributaries from the mouth of Lewis Lake to the mouth of the Henrys Fork, cutthroat trout composed about 8% of their diet, but the exact proportion of Yellowstone cutthroat trout cannot be estimated because this included the range of the Snake River fine-spotted cutthroat trout (unnamed subspecies of cutthroat trout occurring in the Snake River between Jackson Lake and Palisades Reservoir; Behnke 1992).

Thurrow et al. (1988) cited McMasters (1970) and Thurrow (1982) to support their contention that Yellowstone cutthroat trout were opportunistic feeders that consume preferred food items according to availability. Behnke (1992) suggested that Yellowstone cutthroat trout are generally more piscivorous than westslope cutthroat trout. In migratory populations in Idaho, growth increased coincident with a shift from insectivory to piscivory following emigration from the tributaries (Skinner 1985). Because Yellowstone cutthroat trout in Heart Lake (Snake

River drainage, Yellowstone National Park) evolved with seven other fishes, piscivory may have been favored among mature cutthroat trout. Perhaps the fewer indigenous fishes explains why piscivory is rare in Henrys Lake and Yellowstone Lake (Irving 1955; Benson 1961; Jones et al. 1990).

Juvenile Yellowstone cutthroat trout in the pelagic area of Yellowstone Lake feed primarily on zooplankton including *Daphnia shædleri* and *Diaptomus shoshone* (Benson 1961). Mature Yellowstone cutthroat trout move into the littoral zone and remain there throughout the year feeding on zooplankton, larger crustaceans (primarily *Gammarus lacustris* and *Hyalella azteca*), and aquatic insects (Benson 1961; Gresswell and Varley 1988; Jones et al. 1990).

One exception to the limited piscivory in Yellowstone Lake was observed during weir monitoring of the annual Yellowstone cutthroat trout spawning migration in Pelican Creek. Approximately 33% of stomach samples collected from Pelican Creek in 1972 ($n=27$) and 1973 ($n=69$) contained fish (Dean and Varley 1974). Of 65 fish identified from stomach samples, 64 were redbase shiners and 1 was a longnose dace; spawning migrations of these two fishes are believed to roughly coincide with cutthroat trout. Although redbase shiners were routinely netted and released below the trap, relations between handling and piscivory below the weir were not investigated. It is possible that the observed predation by cutthroat trout in Pelican Creek may be an artifact of trapping.

Sixty-four parasitic species are associated with cutthroat trout (Hoffman 1967; Heckmann and Ching 1987), and 18 of these have been collected from Yellowstone cutthroat trout from Yellowstone Lake (Heckmann 1971; Heckmann and Ching 1987). In 1956 and 1957, 55–60% of 10,700 fish from Yellowstone Lake tributaries had parasites (Cope 1958). The prevalence of parasites elsewhere is not well documented (Woodbury 1934; Bangham 1951; Hoffman 1967).

Perhaps the most infamous of the parasites associated with Yellowstone cutthroat trout is the tapeworm found in Yellowstone Lake. There is disagreement about the taxonomy of this tapeworm (Otto and Heckmann 1984). Recent work suggests that two species, *Diphyllbothrium ditremum* and *Diphyllbothrium dendriticum*, are present instead of the single previously identified species *Diphyllbothrium cordiceps* (Heckmann and Ching 1987). Infestation rates are high (46–100%; Woodbury 1934; Bangham 1951; Post

1971; Heckmann and Ching 1987). Effects on mortality rates have not been assessed. Hall (1930) speculated that stunting and diminished egg production were possible, but this has never been substantiated. Some individuals may contain over 400 plerocercoids (Heckmann 1971), but many individuals exhibiting a high level of parasitism often remain vigorous (Post 1971).

The aesthetics of dense infestations of tapeworms appear to be the major concern of anglers (Linton 1891; Post 1971), but there is some evidence that human infections are possible (Heckmann and Ching 1987). Many anglers from Yellowstone Lake historically responded by discarding parasitized fish. In one survey in July 1959, 7,500 fish were counted in garbage cans near Yellowstone Lake. During 4 random days in July 1978, only 9 Yellowstone cutthroat trout were found in almost 300 bags of garbage from 2 campgrounds; expansion of these results yielded an estimate of 300 discarded fish for the 2 campgrounds during the month (Jones et al. 1979). The difference in counts is believed to be associated with reduced infection rates in younger fish that now constitute the legal harvest. The white pelican is a host of the tapeworm (Linton 1891), and during the 1920's, there was support for a plan to destroy pelican eggs on the rookery to reduce the bird population and (hypothetically) the incidence of tapeworms (Varley and Schullery 1983).

Other parasites may be numerous. Parasitic copepods, *Lepeophtheirus salmonis*, *Lernaeopoda bicauliculata*, *Salmincola edwardsii*, and *Salmincola* sp. (Heckmann and Ching 1987), are found on gills, fins, and points of fin insertion. Cope (1958) reported that highest infestation density was at the point of fin insertion. Leeches, *Piscicola salmositica* and *Illinobdella* sp. (Heckmann and Ching 1987), occur on the outside of the body, but there does not appear to be a preferred area (Cope 1958).

One species of eye fluke, *Diplostomum baeri bucculentum*, occurred in all 25 Yellowstone cutthroat trout collected from Yellowstone Lake in 1985 by Heckmann and Ching (1987). Dwyer and Smith (1989) found metacercariae of eye flukes thought to be *Diplostomum baeri bucculentum* in 6 of 10 Yellowstone cutthroat trout from Yellowstone Lake. Eye flukes cause diplostomatosis or eye fluke disease of fishes, and the effect on visual acuity depends on the density of worms (Heckmann and Ching 1987). Severe infections may affect feeding ability and ultimately growth.

Infestation characteristics varied with location, sex, and season. Among spawning migrations in five tributaries, parasite infestation rates appeared to be higher in Arnica Creek than in other tributaries (Cope 1958). Cope (1958) also found that males had more parasitic copepods, females harbored more leeches, infestation rates decreased through time, and fewer downstream migrants were parasitized than were upstream migrants. Yellowstone cutthroat trout in Clear Creek were an exception to this seasonal generalization; the greatest incidence of leeches was during the latter portion of the migration. Since 1978, however, data from Clear Creek suggest higher infestation in the early portion of the migration (USFWS, unpubl. data).

Little is known about disease in naturally reproducing populations of Yellowstone cutthroat trout. The causative agent for furunculosis, *Aeromonas salmonicida*, has been isolated from individuals collected from the Yellowstone River below Yellowstone Lake (USFWS, unpubl. data). MacConnell and Peterson (1992) reported proliferative kidney disease in a population of Yellowstone cutthroat trout in a remote reservoir in Montana, but this was the first substantiated occurrence of the disease in a feral population of cutthroat trout.

Reasons for Concern

Yellowstone cutthroat trout were historically found in the Yellowstone River drainage in Montana and Wyoming and in the Snake River drainage in Wyoming, Idaho, Utah, Nevada, and probably Washington (Varley and Gresswell 1988; Behnke 1992). Human activities and angler harvest have resulted in widespread extirpation of populations of this subspecies. Varley and Gresswell (1988) estimated that genetically unaltered populations of Yellowstone cutthroat trout occupy 10% of the historical stream habitat (2,400 km) and about 85% of the historical lacustrine habitat (38,500 hectares). Presently, 91% of the current range of Yellowstone cutthroat trout lies within the boundary of Yellowstone National Park (Gresswell and Liss, in press).

In contrast to declines of other cutthroat trout subspecies, the decline of Yellowstone cutthroat trout has been well documented. In a summary of the distribution of Yellowstone cutthroat trout in Montana, Hadley (1984) reported a continued loss of Yellowstone cutthroat trout populations from a previous assessment by Hanzel (1959). More recently, biolo-

gists estimated that the subspecies historically occupied approximately 4,800 and 15,100 km of streams in Montana and Wyoming (Yellowstone Cutthroat Trout Working Group 1994). Habitat suitability for Yellowstone cutthroat trout was not verified for all locations identified in Wyoming, thus these may be overestimates. Approximately 965 km of stream in Montana and 4,700 km in Wyoming were assumed to currently support Yellowstone cutthroat trout. These estimates may also be inflated because populations are introgressed in 42–50% of the current habitat in Montana, and there is no information available concerning the genetic purity of Yellowstone cutthroat trout populations in Wyoming (YCTWG 1994). Considering only genetically unaltered populations in Montana, it appears that only 10% of the historical range (stream km) in that state still sustains Yellowstone cutthroat trout. Assuming similar conditions in Wyoming, estimates of the current range by Varley and Gresswell (1988) may be realistic but not encouraging. Significantly, 54% of the existing fluvial habitat of Yellowstone cutthroat trout supports introduced salmonids, e.g., brown trout and brook trout, that are potential competitors or predators.

Population declines and extirpations have been greatest in low-elevation, high-order (3 or larger) streams (Hanzel 1959). These areas have historically been the focus of most human activities including agriculture and resource extraction. Additionally, abundant access in low-elevation areas has encouraged angler harvest and nonnative species introductions. Remoteness of high-elevation portions of the native range probably contributed to the preservation of remaining populations, and in much of this area, public ownership has provided habitat protection that is lacking in lower elevations (Varley and Gresswell 1988).

Causes of the Decline

Hybridization resulting from introductions of rainbow trout, nonnative subspecies of cutthroat trout, or nonindigenous stocks of Yellowstone cutthroat trout is the primary cause of the decline and extirpation of Yellowstone cutthroat trout throughout its historical range (Allendorf and Leary 1988; Varley and Gresswell 1988). Hybrids between rainbow trout and Yellowstone cutthroat trout are developmentally successful, and progeny may appear as morphological and meristic intermediates between parental types or virtually identical to a single parental type (Ferguson et al. 1985). Consequently, it is virtually

impossible to verify genetic integrity with morphological data alone. Nuclear allozymes and mtDNA haplotypes, however, have proven useful for detecting hybridization (Leary et al. 1987; Forbes and Allendorf 1991).

In the upper Snake River drainage, hybridization with rainbow trout has resulted in the virtual disappearance of Yellowstone cutthroat trout in the Henrys Fork Snake River (Griffith 1988) and lower portions of the Blackfoot, Portneuf, and Teton rivers (Varley and Gresswell 1988). In Montana, virtually all drainages where rainbow trout have been stocked in the historical range of Yellowstone cutthroat trout now support hybrid populations of the two species (Hanzel 1959). Allendorf and Leary (1988) reported evidence of hybridization and introgression in 8 of 16 samples from tributaries to the Yellowstone River in Montana. Because these tributaries were selected at random, Allendorf and Leary (1988) asserted that the results were a reliable representation of hybridization in the Yellowstone River drainage.

Reproductive isolation between Yellowstone cutthroat trout and rainbow trout has apparently prevented hybridization in some areas. Wishard et al. (1980) examined Yellowstone cutthroat trout populations from four tributaries to the upper Blackfoot River and found no evidence of hybridization with rainbow trout. In these drainages, Yellowstone cutthroat trout spawn in May and June in headwater reaches, and rainbow trout of hatchery origin typically spawn from winter through spring in lower reaches of the drainage (Thurrow 1982). A similar situation has been observed in the Yellowstone River below the Lower Falls.

Snake River fine-spotted cutthroat trout have been introduced in many waters originally containing Yellowstone cutthroat trout, but the extent of hybridization is unknown, in part because hybrids are difficult to recognize. Introgression resulting from the introduction of mixed stocks of Yellowstone cutthroat trout is also common (Allendorf and Leary 1988). Yellowstone Lake was once the largest source of cutthroat trout in the world, and over 818 million eggs were gathered from Yellowstone Lake tributaries between 1899 and 1957 (Varley 1979). Many of the resulting fry were returned to the lake (Gresswell and Varley 1988; Varley and Gresswell 1988). At the metapopulation level, Gresswell and Varley (1988) suggested that planting fry in the lake and its tributaries led to the potential mixing of up to 68 historically distinct genetic entities.

Non-salmonid species are commonly indicted as competitors of salmonid species, but it does not appear that the introduction of longnose suckers, reidside shiners, and lake chubs into Yellowstone Lake has affected Yellowstone cutthroat trout (Gresswell and Varley 1988). Marrin and Erman (1982) found evidence of competition between brown trout and rainbow trout in Stampede Reservoir, California, but competition between trout and the tui chub or Tahoe sucker was "unlikely." Niche separation, both spatial and temporal, may reduce the incidence of competition in these examples. Although competition may be substantial in different environments, it would probably be greatest between species with similar niches.

Introduction of brown trout and rainbow trout to the Madison River in Yellowstone National Park was followed by the extirpation of indigenous westslope cutthroat trout and fluvial Arctic grayling (Jones et al. 1981), but Yellowstone cutthroat trout are still abundant in sections of the Yellowstone River where they are sympatric with brown trout and rainbow trout (Clancy 1988). In some Idaho streams where Yellowstone cutthroat trout are sympatric with brown trout and brook trout, cutthroat trout persist if habitat has not been degraded and angler harvest is not extreme (Thurow et al. 1988). The consequences of the recent unauthorized introduction of lake trout into Yellowstone Lake are unknown.

Griffith (1988) reported that cutthroat trout are less likely to coexist with brook trout than with other nonnative salmonids even in undisturbed habitats, and Yellowstone cutthroat trout have been extirpated from most areas in Yellowstone National Park where brook trout have been introduced (Gresswell 1991). Mechanisms for replacement are unknown (Griffith 1988; Thurow et al. 1988). Competitive exclusion has probably been cited most frequently, and niche overlap may be greater between Yellowstone cutthroat trout and brook trout than between these fishes and other salmonid species.

Alternatively, species replacement (Griffith 1988) may often explain the extirpation of Yellowstone cutthroat trout. MacPhee (1966) reported that brook trout were less vulnerable to angling than were cutthroat trout. In a section of the Yellowstone River in Montana where special regulations have been imposed (catch-and-release for cutthroat trout; four fish less than 330 mm and one fish greater than 559 mm for brown trout and rainbow trout), the incidence of hooking scars was greater for Yellowstone cutthroat

trout than for brown trout or rainbow trout (Shepard 1992). Differential mortality imposed by angler harvest could contribute to the eventual dominance of the least susceptible group. Once cutthroat trout have been replaced by another salmonid, the situation is generally irreversible without human intervention (Moyle and Vondracek 1985).

Human activities such as dam construction, water diversions, grazing, mineral extraction, road construction, and timber harvest have substantially degraded lotic environments (Meehan 1991), including portions of the historical range of Yellowstone cutthroat trout. Angler wading can also be a significant source of disturbance (Roberts and White 1992). Human activities have resulted in barriers to migration, reduced flows, sediment deposition, groundwater depletion, streambank instability, erosion, and pollution. Efforts to curtail human activities and restore degraded stream segments are increasing, but habitat degradation continues at an alarming rate.

Although there are no dams on the Yellowstone River in the historical range of the Yellowstone cutthroat trout, numerous impoundments in the Snake River have altered historical fish migration patterns. Spawning and rearing areas have been isolated in the Blackfoot, Portneuf, South Fork Snake, Teton, Henrys Fork Snake, and main-stem Snake rivers (Thurow et al. 1988). Below dams, spawning and rearing habitats are limited, and altered discharge patterns compound problems downstream (Thurow et al. 1988). Elle and Gamblin (1993) suggested that reduced winter flows below a dam on the South Fork Snake River resulted in significant mortality of age 0 Yellowstone cutthroat trout.

Culverts can also alter or totally block fish migration (Belford and Gould 1989), and culverts are widespread throughout the range of the Yellowstone cutthroat trout. Belford and Gould (1989) reported that Yellowstone cutthroat trout could not pass through a culvert on Cedar Creek, a tributary to the Yellowstone River in a section where population densities are limited by the availability of spawning habitat (Clancy 1988). Several culverts on tributaries to Yellowstone Lake reduce access to adfluvial spawners, and at least two culverts totally block annual spawning migrations (Dean and Varley 1974; Jones et al. 1986).

Water diversions have been significant in the decline of Yellowstone cutthroat trout in Montana (Hadley 1984). Clancy (1988) found that population density of Yellowstone cutthroat trout in the Yellowstone River was greatest in the vicinity of

tributaries that supported spawning migrations. Byorth (1990) documented loss of spawning habitat for Yellowstone cutthroat trout in three tributaries to the Yellowstone River where water was diverted annually. Irrigation withdrawals often prohibited fluvial migrations into Reese Creek, a tributary to the Yellowstone River on the north boundary of Yellowstone National Park, prior to water-rights adjudication (Jones et al. 1990). In Idaho, the Blackfoot, Henrys Fork Snake, Portneuf, Raft, Teton, and main-stem Snake rivers and Willow Creek are seriously affected by irrigation removals (Thurow et al. 1988). Degraded water quality and unscreened irrigation ditches contribute to the problems associated with water diversions (Johnson 1964; Clancy 1988; Thurow et al. 1988; Byorth 1990).

Effects of livestock grazing on riparian habitats are well documented (Gresswell et al. 1989; Platts 1991). In the range of the Yellowstone cutthroat trout, Thurow et al. (1988) reported that intensive livestock grazing has caused degradation of riparian areas and subsequent stream bank sloughing, channel instability, erosion, and siltation. Alterations are broadly distributed on private and public lands throughout the upper Snake River basin in Idaho and Wyoming (Binns 1977; Thurow et al. 1988). Clancy (Montana Department of Fish, Wildlife, and Parks, pers. commun.) suggested that habitat deterioration resulting from livestock grazing in the Yellowstone River drainage was less of a threat to indigenous populations of Yellowstone cutthroat trout than hybridization and dewatering.

The influence of mineral extraction on Yellowstone cutthroat trout in Idaho has been primarily within the Blackfoot River drainage. Phosphate mines in that area are associated with increased sedimentation (Thurow et al. 1988). An abandoned gold mine in the headwaters of Soda Butte Creek (near Cooke City, Montana, upstream from Yellowstone National Park) caused extensive pollution through the 1960's (Jones et al. 1982). In Yellowstone National Park, fish populations were low, and anglers had minimal success (Arnold and Sharpe 1967). Reclamation of the tailings site reduced the input of pollutants and led to improvements in the fishery during the last two decades (Jones et al. 1982). A planned expansion of mining near Cooke City poses a renewed threat to the Yellowstone cutthroat trout population in Soda Butte Creek (Jones et al. 1992).

Yellowstone cutthroat trout are extremely vulnerable to angling, and angler harvest has contributed

to substantial declines in population abundance throughout the historical range of the subspecies (Binns 1977; Hadley 1984; Gresswell and Varley 1988; Thurow et al. 1988). Schill et al. (1986) estimated that individuals in the Yellowstone River between Yellowstone Lake and Sulphur Caldron were captured an average of 9.7 times during the 108-day angling season. Many tagged Yellowstone cutthroat trout were captured two or three times in a single day (Schill et al. 1986). Although high catchability is important to most anglers, it may lead to substantial declines in abundance if the harvest is not restricted (Gresswell and Liss, in press).

Examples from Yellowstone National Park have special relevance because anthropogenic habitat alterations have been minimal. In Yellowstone Lake, measures of abundance and population structure of Yellowstone cutthroat trout suggested substantial deviation from historical levels as harvest increased through the 1950s. By 1968, landing rate and average size of captured fish declined to unprecedented levels (Gresswell and Varley 1988). These changes happened under a creel limit of only three fish per day; angler effort during this period reached 15.8 angler-hours/ha (Varley and Gresswell 1988). Similar effects were noted on populations in the Yellowstone River (Fishing Bridge-Upper Falls) and Lamar River. Following implementation of special regulations, these populations exhibited significant increases in mean length and generally stable landing rates despite continued increases in angler effort (Gresswell and Varley 1988; Gresswell and Liss, in press).

Outside of Yellowstone National Park, effects of angler harvest have been similar. The mean length and the proportion of spawners greater than 380 mm declined substantially between 1973 and 1983 in Cedar Creek. During that period angling regulations allowed the daily harvest of 5 Yellowstone cutthroat trout (only one over 457 mm). Beginning in 1984, regulations for Yellowstone cutthroat trout in the Yellowstone River for approximately 80 km downstream from the Park boundary were changed to catch-and-release. Clancy (1988) reported an increase in the proportion of Yellowstone cutthroat trout larger than 299 mm in that section of river since the implementation of the no-harvest regulation and Shepard (1992) suggested that density increased where recruitment of Yellowstone cutthroat trout was adequate (Shepard 1992). The proportion of Yellowstone cutthroat trout longer than 405 mm had not increased significantly by 1991 (Shepard 1992).

Thurrow et al. (1988) suggested that angler harvest had contributed to the decline of Yellowstone cutthroat trout in the upper Snake River basin. Special regulations including size limits and adjustments of angling-season length have been implemented on the South Fork Snake and Blackfoot rivers to reduce the effect of angler harvest. A regulation specifying a 2-fish limit and release of Yellowstone cutthroat trout between 250 and 405 mm resulted in an increase in older and larger fish in the South Fork Snake River (Heise to Palisades Dam) after 3 years (Thurrow et al. 1988). In the Blackfoot River, however, a reduced harvest (3-fish limit) without size restrictions did not accomplish management goals (Thurrow et al. 1988).

There is some evidence that historical egg-taking was detrimental to individual spawning populations. Spawning runs were blocked annually in some larger tributaries (Gresswell and Varley 1988). Annual spawner counts in Clear Creek dropped from approximately 16,000 between 1945 and 1948 to 3,353 in 1953 (Benson and Bulkley 1963). After egg-taking ceased in 1953, the number of Yellowstone cutthroat trout spawners rose to an average of 7,300 annually between 1957 and 1961 (Gresswell and Varley 1988). By the mid-1960's spawner counts had reached an average of 36,000 annually, despite concurrent increases in angler harvest in the lake (Gresswell et al., in press).

Current Management

Yellowstone cutthroat trout have been designated as a "Species of Special Concern-Class A" by the American Fisheries Society (Johnson 1987), and this status has been officially recognized by the Montana Department of Fish, Wildlife, and Parks (YCTWG 1994). The subspecies is also recognized as a species of special concern in Idaho and managed accordingly. Both the Northern and Rocky Mountain regions of the USDA Forest Service consider the Yellowstone cutthroat trout a sensitive species (YCTWG 1994). Though the Yellowstone cutthroat trout has not been given a formal status in Wyoming, the subspecies has influenced management activities in recent years (YCTWG 1994; R. Wiley, Wyoming Game and Fish Department, pers. commun.). In Yellowstone National Park, indigenous species, including the Yellowstone cutthroat trout, receive priority in management decisions.

Concerned management agencies in Wyoming and Montana recently developed a draft interagency

management guide for the Yellowstone River basin (YCTWG 1994). The guide formalized management strategies for the Yellowstone cutthroat trout in the Yellowstone River basin and clarified the direction of management for the subspecies. Supporters of the plan included the American Fisheries Society, Bureau of Land Management, Crow Indian Tribe, Greater Yellowstone Coalition, Montana Association of Conservation Districts, the National Park Service, Trout Unlimited, USDA Forest Service, and the USDI Fish and Wildlife Service.

Special status provided to indigenous populations of Yellowstone cutthroat trout is critical to the fish's persistence. Current management emphasizes populations sustained by natural reproduction and by stocking (Varley and Gresswell 1988; YCTWG 1994). Both management approaches include strategic elements involving genetic integrity, habitat management, and harvest regulation (Varley and Gresswell 1988).

Efforts to identify genetically unaltered populations of Yellowstone cutthroat trout are important. In the Yellowstone River drainage, both in Yellowstone National Park and outside the Park in Montana, genetic sampling has been pursued vigorously in recent years. Most management agencies require positive genetic identification before protecting populations of Yellowstone cutthroat trout, so this work is critical to the persistence of the subspecies (Varley and Gresswell 1988). Additionally, the value of protecting and genetically restoring introgressed populations of Yellowstone cutthroat trout where genetic purity is greater than 97% was officially recognized in the interagency management guide for the Yellowstone River basin (YCTWG 1994).

To maintain genetic integrity of indigenous populations of the Yellowstone cutthroat trout, Montana, Idaho, and Wyoming have modified their stocking guidelines. Management of fluvial fisheries in Montana emphasizes wild trout populations, and stocking in lotic systems was terminated in 1974 (Vincent 1987). In Idaho, stocking in the upper Snake River basin is restricted to waters that do not support viable populations of genetically unaltered Yellowstone cutthroat trout. In areas that still receive nonnative fish introductions, tactics to prevent introgression are being investigated (Thurrow et al. 1988).

The use of piscicides to remove undesirable fishes to protect indigenous species from hybridization and competition with other salmonid species has been infrequent (Rinne and Turner 1991). In Colorado and Montana this technique has been successfully used

to protect and reestablish indigenous cutthroat trout populations. In Yellowstone National Park, brook trout were removed from Arnica Creek, a tributary to Yellowstone Lake that supports an annual migration of adfluvial Yellowstone cutthroat trout (Gresswell 1991). Renovation eliminated potential competition and predation in Arnica Creek and prevented the invasion of the lake and other tributaries by brook trout. Although removal of nonnative species may be critical for protecting and reintroducing Yellowstone cutthroat trout in some areas, it is extremely expensive and difficult to achieve; the preferred alternative is to avoid nonnative species introductions.

Varley and Gresswell (1988) suggested that habitat management includes protection, enhancement, and improvement. Protection of habitat may be the most cost-effective form of habitat management. Although improvement is associated with both degraded and relatively pristine habitats, enhancement is generally synonymous with restoring degraded habitats. Opportunities for habitat restoration are widespread, and this activity may significantly affect the persistence of Yellowstone cutthroat trout in their historical range. The USDA Forest Service has recently increased efforts to identify areas of critical habitat for the Yellowstone cutthroat trout in the Greater Yellowstone Ecosystem (B. May, Gallatin National Forest, pers. commun.). Critical habitat will be prioritized for protection and restoration projects.

Modifying culverts is one aspect of habitat enhancement that is often overlooked, but this type of restoration may provide substantial benefits in areas where production is limited. Clancy and Reichmuth (1990) described a detachable fishway that was inexpensive, portable, and durable. Belford and Gould (1989) documented an increase in the number of Yellowstone cutthroat trout spawners ascending a modified culvert in Cedar Creek. They developed guidelines for installing new culverts and identifying culverts that require velocity-reduction devices to allow passage. Wooden baffles were installed in four culverts on two tributaries to Yellowstone Lake in 1976 (Jones et al. 1977). Observations suggest improved passage through these culverts, but effects have not been rigorously evaluated.

Water diversion continues to be a critical aspect of habitat management for the Yellowstone cutthroat trout; unfortunately, it is also one of the most contentious. Attempts have been made to establish fish and wildlife sustenance as a "beneficial use" of flow-

ing water in western states (Varley and Gresswell 1988). In Montana, the Department of Fish, Wildlife, and Parks was recently granted the legal right to lease water rights from agricultural interests, but the use of this strategy has been limited.

Riparian habitats have received increasing management attention since the late 1970's (Platts and Rinne 1985). In recent years, many grazing strategies have been evaluated (Meyers 1989; Platts 1989), and successful techniques are being implemented on many public lands. Improved riparian management may be the most critical habitat issue facing fishery managers in areas where natural flow regimes are unaffected by water diversions.

Gresswell (1990) defined special regulations as number limits, size limits, and terminal gear specifications, used singly or collectively, to reduce angler harvest. Season length and fishing season opening date are important auxiliary mechanisms that can be used to protect vulnerable spawning aggregations. Currently, these regulations are being broadly applied within the present range of the Yellowstone cutthroat trout to maintain indigenous and introduced populations. A combination of size limits and daily creel and possession limits are being used in Yellowstone National Park. Catch-and-release regulations are the most common, but in some areas maximum- (only fish below a specified size may be kept) and minimum-size (only fish above a specified size may be kept) limits are used in conjunction with a 2-fish creel limit. In Idaho, harvest of Yellowstone cutthroat trout on the South Fork Snake River from Heise to Palisades Dam is limited to 2 fish; fish between 203 and 406 mm must be released (Elle and Gamblin 1993). Reduced angling seasons and harvest limits (2 to 3 fish) are being considered for Henrys Lake and the Blackfoot River (Thurrow et al. 1988). Yellowstone cutthroat trout are protected either by catch-and-release or 2-fish slot limits in Montana, and in Wyoming, 2-fish (any size) and 2-fish slot limits have been implemented for most indigenous populations. In 1994 the catch-and-release regulation in Montana was extended to include all streams and rivers in the Yellowstone River basin upstream from Springdale, Montana, to the Yellowstone National Park boundary (YCTWG 1994).

Research Needs

The relation between life history variation and environmental characteristics merits investigation, as

do age-specific habitat needs. Identifying large-scale habitat factors that influence distribution, dispersal, and recolonization of Yellowstone cutthroat trout is also crucial for evaluating the effects of current land-use activities and anticipated global climate change.

Knowledge of life history diversity (and whether it has a genetic basis) is critical to protecting the remaining populations of Yellowstone cutthroat trout. Varley and Gresswell (1988) suggested that the greatest threat to the subspecies was the continued loss in genetic variability represented by unique local populations. Considering efforts to preserve genetic diversity, Echelle (1991) cautioned that no single measure of diversity, e.g., mtDNA, meristics, or life history variation, should take precedence over other forms of information. Identifying differences among populations can provide important information concerning local adaptation and the relation between life history organization and specific aspects of habitat.

To understand the natural capacity of the Yellowstone cutthroat trout, it is important to evaluate life history strategies and organization in areas where the effects of human activities can be minimized. Most information concerning Yellowstone cutthroat trout has focused on maintaining angler harvest, thus there are relatively few data on undisturbed populations. Often, angler harvest has been neglected in research design despite its influence. Although there are abundant data from Yellowstone Lake describing Yellowstone cutthroat trout life history during the 1950's, this was a period when the influence of cultured fish and angler harvest was at a maximum. Also, research is needed to assess the indirect effects of angling, such as redd trampling and bank erosion.

Long-term monitoring is integral to understanding the variation in Yellowstone cutthroat trout populations and relations between habitat and climatic variation. Such monitoring is essential for determining the effects of angler harvest and long-term habitat changes.

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Synthesis of Management and Research Considerations

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The five subspecies of cutthroat trout considered in this assessment share one characteristic: the loss of populations throughout their historical ranges. Similar causes have led to these losses: the introduction of nonnative fishes, overharvest, habitat degradation, and probably habitat fragmentation. Synergism among these effects remains unstudied, and we do not understand the biology of some of these subspecies, hence our ability to reverse the loss of populations is handicapped. Ironically, such ignorance has been inappropriately interpreted as a reason to avoid management action until more research is conducted, risking the loss of these subspecies in the interim (cf. Nehlsen et al. 1991).

Nonnative Fishes and Stocks

The effects of introducing nonnative fishes depends on the species introduced. That subspecies of cutthroat trout will readily hybridize with rainbow trout or with other cutthroat trout subspecies is widely acknowledged (and is probably attributable to polyploidy in salmonids; Allendorf and Leary 1988). Yet the geographic extent of genetically pure populations (or some subspecies) is virtually unknown, because few populations from each subspecies have been examined with techniques sensitive to minor amounts of hybridization. Lack of thorough testing has led to some embarrassment; genetic analysis of a supposedly pure population of Colorado River cutthroat trout in Utah, recognized in the recovery plan as one of the few known populations in the state, revealed it to be a stocked population of Yellowstone cutthroat trout (Shiozawa et al. 1993). Some populations appear to have resisted hybridization despite the presence of nonnative congeneric fishes (Trojnar and Behnke 1974; Utter et al. 1989); this resistance may be related to reproductive isolating mechanisms, our inability to detect hybridization (such as between fine-spotted cutthroat trout and

Yellowstone cutthroat trout), or chance. Understanding these mechanisms might help us protect other populations exposed to closely related nonnative fishes.

We know that certain populations of cutthroat trout contain foreign genes. Depending on the rarity of the subspecies, such hybrid populations may merit preservation as the best remaining examples of the entire subspecies (O'Brien and Mayr 1991; Dowling and Childs 1992) or of evolutionarily significant units (sensu Waples 1991) of the subspecies. For this reason, Wyoming has adopted policies protecting partially hybridized populations of Colorado River cutthroat trout, as has the Yellowstone Cutthroat Trout Working Group (1994). Alternatively, such populations are often proposed for extermination if they can be refounded with genetically pure stocks.

Brook trout or brown trout introductions have almost always led to the replacement of cutthroat trout populations. Though competition has been speculated as the cause of replacement, especially by brook trout, researchers have failed to identify the life stage or specific competitive mechanism(s) that lead to this replacement (cf. Fausch 1988, 1989). Replacement of cutthroat trout by brown trout has been less studied and is also poorly understood. Again, some populations of cutthroat trout, particularly of westslope and Yellowstone cutthroat trout, have persisted despite the presence of these nonnative fishes, and understanding why might help us preserve other populations. That such persistence may be related to the evolutionary exposure of cutthroat trout subspecies to certain guilds of other fishes merits attention.

Even transfers of a subspecies within its indigenous range may be undesirable. Adjacent populations of both westslope cutthroat trout (Allendorf and Leary 1988) and Colorado River cutthroat trout (Leary et al. 1993) were found to be genetically distinct. Interbasin transfers could lead to genetic mixing and the loss of locally adapted stocks (Scudder

1989). For example, transfers of adfluvial Yellowstone cutthroat trout from Yellowstone Lake to streams containing fluvial and resident stocks in other watersheds may have contributed to the loss of unique stream-adapted genomes, but it is doubtful we will ever know because this stocking was widespread. As a final caution, if neighboring populations differ genetically, we must consider whether those differences naturally evolved or resulted from anthropogenic isolation (Fausch and Young, in press).

"Ideal" Habitat

Degraded habitat, caused by natural forces or land management, is among the most frequently identified causes of extirpated or diminished cutthroat trout populations. Actual losses of habitat, caused by water diversion, log drives, channelization, urbanization, or mining pollution, are obvious problems. But the effects of indirect activities, such as logging, livestock grazing, or recreation, have been more difficult to quantify, and their contribution to the loss of populations is equivocal.

Though we understand the basic habitat components, we know little about what constitutes "ideal" habitat for any subspecies. The presence of populations of indigenous cutthroat trout in high-elevation, low-order streams has led to suggestions that these habitats are optimal (Griffith 1988), though these streams might be viewed as among the most marginal habitats owing to their small size, short growing seasons, and environmental extremes (Lawton 1993). Because populations are largely constrained to these habitats, identifying what is preferred for occupation becomes difficult (Ruggiero et al. 1988). Nevertheless, historical accounts indicate that these fish once occupied much larger, more productive waters: Lewis and Clark captured westslope cutthroat trout in 1805 in the Missouri River near Great Falls, Montana; Bonneville cutthroat trout were abundant in Utah Lake in the late 1700's; and Colorado River cutthroat trout occupied the Green River into the 1900s. Apparently human activities, directly or indirectly, have restricted most populations to small watersheds, many of which retain pristine fish communities and habitat (Rieman and Apperson 1989). Baltz and Moyle (1993) suggested that fishes in pristine habitats are more resistant to invasion by non-native fishes, but this assertion is largely untested for many cutthroat trout subspecies, and examples to the contrary abound (papers in this volume).

There is some question on how to select the dependent variable to define what is "ideal" habitat. Almost without exception, fisheries biologists have considered the best habitat to be the one containing the greatest density or biomass of fish; virtually all models of habitat quality use density or biomass as the dependent variable (cf. Fausch et al. 1988). But Van Horne (1983) noted that animal density did not always reflect habitat quality; seasonal changes in habitat use, patchy habitats, or time lags between habitat quality and fish response could lead to a decoupling of the habitat quality-fish density relation. Similarly, Fretwell (1972) suggested that territorial defense by competitively dominant individuals could lead to greater occupation of suboptimal habitats by subdominants. Consequently, future evaluations of habitat should consider alternative indices for defining habitat quality, e.g., the population age structure, or measures of habitat characteristics that confer persistence, resilience, or stability to fish populations at the appropriate spatial and temporal scale.

I perceive, perhaps incorrectly, that many biologists regard lotic habitats as static, i.e., once the desired habitat quality and quantity is established, it will remain essentially unchanged for years. But watersheds constantly change (e.g., vegetative succession or beaver, *Castor canadensis*, invasion) and will undergo natural disturbances at unpredictable intervals (e.g., intense wildfire or 500-year floods), and fish populations must respond to the eventual changes in terrestrial, riparian, and channel characteristics. Even if we could recognize optimal habitat, maintaining it in a single stream indefinitely is fighting against natural processes, and is inconsistent with land management reform directed at maintaining plant and animal communities in perpetuity (i.e., ecosystem management; Grumbine 1994). By working with these processes, we may be able to create a mosaic of watershed ages in larger systems that will maintain optimal habitat in different portions of the basin at various times and that could provide largely suitable habitat elsewhere (cf. Pringle et al. 1988). This suitable habitat should include refugia from environmental or anthropogenic disturbance that serve as sources for recolonization (Sedell et al. 1990). The kind of refugia necessary to resist some disturbances may be obvious, e.g., deep pools during drought or groundwater upwelling during thermal extremes, but the number and complexity of refugia needed for long-term persistence is unknown.

That trout would move to and from refugia contradicts the prevailing dogma that most stream-dwelling cutthroat trout are relatively sedentary and have all of their life history needs met in small reaches, even single pools, of streams (Miller 1957; Heggenes et al. 1991; Behnke 1992). Recent research has demonstrated that many individuals move substantial distances, even within a 24-hour cycle (Young, unpubl. data). Failing to recognize the mobility of these fish could invalidate past estimates of population size and confound our ability to determine population trends (cf. Decker and Erman 1992). Consequently, we should understand when these fish move, what habitats they are moving to, and how much of a stream or how many streams they require to fulfill their life history needs.

Metapopulations

Movement may be especially critical because some populations of cutthroat trout (especially westslope and Yellowstone cutthroat trout on federally protected lands) appear to form metapopulations. Metapopulations consist of a collection of subpopulations that are linked by immigration and emigration (Hanski and Gilpin 1991). The individual subpopulations may thrive, suffer losses of genetic variation, or go extinct, but individuals from other subpopulations within the metapopulation can contribute to the growing subpopulations, restore genetic variation to small subpopulations, or found new subpopulations after extinction. The diversity of life history strategies, subpopulation dynamics, and the structure of these apparent metapopulations of cutthroat trout are unknown. Several kinds of metapopulation structures exist, depending on the interactions among subpopulation sizes, habitat area and quality, and immigration and emigration patterns, and these structures have different implications for species persistence and reserve designs (Harrison 1991).

To persist, metapopulations must consist of mobile individuals in habitats without continuous barriers to movement, and some subpopulations must escape particular environmental events that affect other subpopulations (Gilpin 1987). The linear arrangement of streams provides connectivity between subpopulations, but with two risks. First, diseases or introduced species may spread via the corridors (Simberloff 1988). Second, environmental variation can be correlated because both upstream and down-

stream characteristics, activities, and fish communities may influence an intermediate reach (Vannote et al. 1980; Osborne and Wiley 1992).

Whether cutthroat trout form metapopulations is controversial and speculative. Based on genetic evidence, Allendorf and Leary (1988) and Shiozawa and Evans (1994) concluded that populations of some subspecies of cutthroat trout are largely nonmigratory; the logical extension of this contention is that these subspecies did not form metapopulations in some streams. Nevertheless, whether cutthroat trout form metapopulations (and what metapopulation structure develops) has never been directly investigated.

For most populations of cutthroat trout, the question of metapopulation dynamics is moot: connectivity to other populations has been lost and will be difficult to restore without stream restoration or non-native fish eradication. For these populations, management and research focusing on population viability, genetic drift, inbreeding depression, and extinction probabilities is paramount.

Extinction Factors

Several rules of thumb have been developed to estimate the adult population sizes needed to avoid extinction, though these rules are widely debated (Soulé 1987; Simberloff 1988; Boyce 1992). Their application is controversial because the consequences of violating these rules are primarily based on theory, not empirical evidence (Caro and Laurenson 1994; Caughley 1994). Also, the persistence of small populations of desert fishes for thousands of years (Minckley and Deacon 1991) challenges the relevance of these rules. Nevertheless, they are applied, perhaps because they offer a quantifiable target for recovery. Theoretically, demographic uncertainty, as reflected by chance individual variation in survival and reproduction, becomes less problematic once populations exceed 30 to 50 individuals (Boyce 1992). "Allee effects," which are density-dependent effects such as the difficulty in finding mates, also apply when populations are very small (Simberloff 1988). Inbreeding depression, caused by the expression of deleterious alleles, may be avoided if effective population sizes exceed 50 to 60 adult animals (Franklin 1980; Ryman and Ståhl 1980; Soulé 1987). But note that effective population sizes are almost always less than total population sizes, sometimes much less (Futuyma 1986). Alternatively, populations that survive numerical bottlenecks may avoid later inbreed-

ing depression because deleterious alleles will have been purged (Caughley 1994). To avoid the loss of genetic variation in quantitative traits (and maintain long-term adaptability to environmental change), effective populations of around 500 adults may be necessary (Franklin 1980; Lande and Barrowclough 1987).

In contrast, population extinctions from environmental changes, whether deterministic or stochastic, have been amply demonstrated. Over scales of a few years to centuries, most populations are at much greater risk from extinction from environmental stochasticity than from demographic or genetic causes (Shaffer 1987), and increasing the frequency of environmental disturbance increases the probability of extinction (Boyce 1992). Eventually, populations reduced by environmental variation also risk extinction from demographic stochasticity or the loss of genetic variation. Similarly, deterministic events, such as habitat loss, overfishing, or introductions of nonnative fish, may drive populations down and heighten their vulnerability to all stochastic risks (Gilpin and Soulé 1986; Rieman and McIntyre 1993). Generally, the smaller the population and more variable the environment, the greater the probability of extinction.

But if environmental changes are catastrophic, extinction may be probable regardless of the size of the population (Shaffer 1987; Mangel and Tier 1994). For example, Propst et al. (1992) estimated there were almost 4,000 Gila trout in Main Diamond Creek in New Mexico in the late 1980s (ironically, the size and number of populations had convinced managers to pursue downlisting of this species from endangered to threatened; P.R. Turner, New Mexico State University, pers. commun.). Immediately after a fire had burned a portion of the Main Diamond Creek watershed in 1989, a rainstorm apparently caused flooding and toxic ash flows that exterminated the Main Diamond Creek population (other than 566 fish that were rescued during the fire and sent to a hatchery). Because this stream is separated from any other perennial stream containing this species, Gila trout failed to recolonize it. An adjacent watershed, South Diamond Creek, was also burned, and the sampled population declined from over 1,000 fish to fewer than 40. Similar fates for many isolated populations of cutthroat trout might be expected.

McIntyre and Rieman (this volume) speculated that populations of cutthroat trout of fewer than 2,000 individuals face a substantially higher risk of extinction than do larger populations. Many populations of the subspecies considered here fall below that

level. Allendorf (1988) suggested that cutthroat trout may be at further risk because their large phenotypic variation and low heritability of traits sensitizes them to environmental conditions and potentially to environmental variation. Also, Dennis et al. (1991) and Nunney and Campbell (1993) suggested that population variability was correlated with the probability of persistence, and populations of trout are thought to fluctuate widely (mean annual fluctuation = 138%, maximum annual fluctuation = 1,073% in 10 western streams; Platts and Nelson 1988). Therefore, if we disregard the effects of movement on population estimates, many cutthroat trout populations would seem prone to extinction. Unfortunately, most studies of extinction probabilities have focused on mammals, birds, and invertebrates (e.g., Murphy et al. 1990; Dennis et al. 1991; Harrison 1991; Stacey and Taper 1992), and their life history characteristics are very different from those of fishes (cf. Thomas 1990). To further complicate the issue, cutthroat trout may tolerate large environmental variation; for example, the number and timing of annual spawning runs depended on the variability in peak flows in a Nevada stream (Nelson et al. 1987). Moreover, cutthroat trout have survived catastrophic environmental changes; this species persisted in a stream exposed to the Mount St. Helens eruption by occupying refugia, presumably habitats created by coarse woody debris (Hawkins and Sedell 1990). Until we understand how life history characteristics, phenotypic plasticity, population structure, and disturbances affect persistence, the probability of extinction of populations is largely speculative.

Conservation Considerations

Because all five subspecies of cutthroat trout continue to decline, ideally all remaining populations, regardless of size, should be conserved to maintain the full genetic variation within each subspecies (Allendorf and Leary 1988). Yet this straightforward guidance presents myriad problems. For example, managers commonly install expensive, permanent barriers on streams containing cutthroat trout to prevent the upstream migration of introduced species. Though effective, these barriers must be regularly maintained at some cost. Furthermore, they isolate cutthroat trout populations from other populations (and possibly from critical habitats), and these populations then risk losses of heterozygosity from genetic drift and are vulnerable to extinction caused by fire,

drought, toxic spills, road failures, or debris torrents (Propst et al. 1992). Extinct populations of cutthroat trout may be reestablished by stocking (another cost), but a hatchery stock (founded and maintained at some expense) will be less well adapted to a watershed than the indigenous stock (Krueger and May 1991; Demarais et al. 1993) and may be even more susceptible to future extinction. Finally, biologists have also failed to acknowledge the consequences of barriers for other aquatic biota; the near complete lack of information should be cause for caution.

Alternatives to "blocking and stocking" merit consideration. Griffith et al. (1989) found that translocations of wild-caught animals were about twice as successful at establishing new populations as were captive-reared animals. Also, transfers of nearby, genetically pure, wild stocks to refound extinct populations avoid the artificial selection and genetic drift often associated with hatchery rearing (Waples and Teel 1990) and may be cheaper. Such transfers also maintain the genetic integrity of locally evolved populations of each subspecies (Shiozawa and Evans 1994). Barriers will probably remain essential, but should be viewed as temporary measures used to prevent invasion before movement corridors are reopened. Reconnecting watersheds should decrease the probability of extinction of all populations and may entail fewer direct costs, but mandates vigilance against the introduction of nonnative fishes or pathogens and is more difficult to establish politically. Also, we should avoid reconnecting genetically distinct endemic stocks; Scudder (1989) argues that the most isolated populations may be the most evolutionarily valuable, because they may have been subjected to the most rigorous selection. But Propst et al. (1992) argued that human-induced isolation has led to genetically unique stocks of Gila trout, and that these stocks should be recombined before being introduced elsewhere.

Given these caveats, managers still have at least three sound tactics for ensuring the persistence of these five subspecies of cutthroat trout: (1) extensively survey streams within their historical ranges to identify remaining populations and highlight unique ones (Leopold's first rule of intelligent tinkering); (2) reestablish probable metapopulations disrupted by human activities (assuming that long-isolated populations can produce migrant individuals); and (3) protect and expand these populations within their historical ranges by including well-distributed refugia, essential habitats, and movement corridors in designated aquatic habitat reserves (for details, see

Frissell 1993; Rieman and McIntyre 1993; Moyle and Yoshiyama 1994).

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